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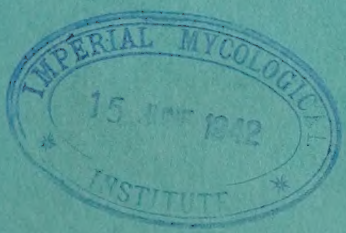
MICHIGAN ACADEMY OF SCIENCE ARTS AND LETTERS

XXVII (1941)

PART II: ZOOLOGY



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MICHIGAN ACADEMY OF SCIENCE ARTS AND LETTERS

VOLUME XXVII (1941)

PART II: ZOOLOGY

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PART I: BOTANY AND FORESTRY

PART II: ZOOLOGY

PART III: GEOGRAPHY AND GEOLOGY

PART IV: GENERAL SECTION

Anthropology, History and Political Science, Language and Literature, Medical Science, Sociology

PAPERS OF THE MICHIGAN ACADEMY OF SCIENCE ARTS AND LETTERS

EDITORS
EUGENE S. McCARTNEY
WILLIAM C. STEERE

VOLUME XXVII (1941)
PART II: ZOOLOGY

"Pusilla res mundus est nisi in illo
quod quaerat omnis mundus habeat."
— SENECA, *Naturales Quaestiones*

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CONTENTS

PAGE

Alabama Spiders of the Family Mimetidae. Allan F. Archer ... 183

Independent Inheritance of Certain Characters in the Deer Mouse, *Peromyscus maniculatus*. Elizabeth Barto 195

Mating of the Garter Snake *Thamnophis sirtalis sirtalis* (Linnaeus). Frank N. Blanchard and Frieda Cobb Blanchard 215

The Palpimanidae of Panama. Arthur M. Chickering..... 235

Age and Growth of the Yellow Perch, *Perca flavescens* (Mitchill), in the Wisconsin Waters of Green Bay and Northern Lake Michigan. Ralph Hile and Frank W. Jobes... 241

Hybridization in Nature between Two Genera of Flounders in Japan. Carl L. Hubbs and Katsuzo Kuronuma..... 267

The Age and Growth of the Lake Erie White Bass, *Lepibema chrysops* (Rafinesque). John Van Oosten..... 307

ILLUSTRATIONS

PLATES

FACING PAGE

HUBBS AND KURONUMA: Pls. I–IV. *Kareius bicoloratus, Platichthys stellatus,* and hybrids 306

FIGURES IN THE TEXT

PAGE

ARCHER: Figs. 1–3. *Mimetus tillandsiae, Ero lodingi, E. pensacolae* 190, 192–193

CHICKERING: Figs. 1–5. External anatomy of *Otiothops macleayi* Banks 236

HILE AND JOBES:

Fig. 1. Localities in Green Bay and Lake Michigan at which samples of yellow perch were taken 242

Figs. 2–4. Charts giving data on yellow perch caught in Green Bay, Saginaw Bay, Lake Erie, and Lake Michigan 259, 262, 264

HUBBS AND KURONUMA:

Figs. 1–2. Maps showing the overlapping distribution of *Kareius bicoloratus* and *Platichthys stellatus,* and the Asiatic localities where the interspecific hybrids were secured 271

Figs. 3–4. Charts showing the average values ("hybrid indices") for the *Kareius* × *Platichthys* hybrids and the intermediacy of the hybrids 292–293

Fig. 5. Lower pharyngeal bones and teeth in Japanese specimens of *Kareius,* hybrids, and *Platichthys* 295

VAN OOSTEN: Figs. 1–4. Charts giving data on Lake Erie white bass 311, 320, 322, 325

ZOOLOGY

ALABAMA SPIDERS OF THE FAMILY MIMETIDAE

ALLAN F. ARCHER

IN 1939 and 1940 I collected an extensive series of Mimetidae in Alabama while making an inventory of spiders under the auspices of the State Department of Conservation. The members of this family are of interest on account of their habits, habitats, and distribution. Only two genera, *Mimetus* and *Ero*, are known to occur in Alabama. *Mimetus* preys exclusively on spiders, many species of which are useful in controlling insect populations. Little information is available about the prey of *Ero*.

The family Mimetidae may be described briefly as follows: three claws, the first and second tibia and metatarsus provided with a row of long spines, the interspaces between which are occupied by a row of much shorter spines.[1] The chelicerae lack a boss (lateral condyle), and the palpus of the female has a terminal claw. Petrunkevitch[2] places the Mimetidae in the group of three-clawed spiders (Trionychae), close to the Archaeidae, Palpimanidae, and Uloboridae, but interposes between this group of families and the Argiopidae a whole series of families, such as the Amaurobiidae, Agelenidae, and Lycosidae. I do not believe that the present evidence warrants this arrangement, and I prefer to follow Bristowe,[3] who classes the Mimetidae close to the Argiopidae in the upper rank of Ecribellatae.

The two Alabama genera may be separated as follows:

1. Legs I and II much longer than legs III and IV; clypeus definitely shallower than the ocular region ..... *Mimetus*
2. Legs I and II very little shorter than legs III and IV; clypeus not shallower than the ocular region ..... *Ero*

In general, the species of *Mimetus* are of greater stature than those of *Ero*, and are a little slower in their locomotion. *Ero* apparently makes a web, but *Mimetus* is not known to do so.

[1] There are some departures from this arrangement of spines in certain exotic genera.

[2] Petrunkevitch, A., *Trans. Conn. Acad. Sci.*, 33: 144, 160–161. 1940.

[3] Bristowe, W. S., *Proc. Zool. Soc. London*, 108: Part 2, 285–321. 1938.

MIMETUS Hentz, 1832

The author of the genus *Mimetus* at first believed its web combined features of the webs of *Aranea* and *Theridion*. He based his belief on the fact that his first specimen was found in the web of *Metepeira labyrinthea* (Hentz), which makes a web of exactly this type. The epigynum of the females of *Mimetus* is in the form of a caudally projecting chitinized lobe. The male palpus has a chitinized cymbium. This genus is widely distributed in Alabama, but fortunately for the spiders which fall prey to the several species, they are not very abundant in any one locality. Although generally slow in its movements, each spider displays great cleverness in stalking its quarry. Apparently its invasion of a nest or retreat usually takes the occupant by surprise. Even when the inhabitant is on guard it attacks aggressively, and is quite capable of killing spiders larger than itself. When protecting its eggs it keeps very quiet, with its legs drawn up. Not infrequently the female remains in the web of her victim, and lays her eggs in it. On a number of occasions I found, much to my amazement, gravid females of *Mimetus* occupying nests of other species of spiders.

In 1923 Chamberlin [4] completely revised the North American species of *Mimetus*. Since then several more species have been described. We now have a large series of locality records from both Alabama and Texas. The Alabama series has enabled me to clear up certain doubtful matters, particularly the correlation between color patterns and the identification of species, which is based on Chamberlin's study of the genitalia. Although there is a certain amount of variation in the color pattern of each species (especially in the males), the limits of variation are rather definite. Chamberlin found that there are two common species in the southeastern states. He determined the identity of one of them, *M. interfector*, on the basis of the male and the palpus, as shown by Hentz,[5] Plate 15, Figure 13. The color pattern and the external morphology of the female in Figure 12 show that it is not of the same species as the male in Figure 13. Since it is the right of the first reviser to fix the species in question and since there is no such thing as figure priority,

[4] Chamberlin, R. V., *Journ. Entomol., Pomona College*, 15: 3–6, figs. 1, 6. 1923.

[5] Hentz, N. M., *Journ. Boston Soc. Nat. Hist.*, 6: 3. 1850.

Chamberlin's decision must stand. The immature male shown in Figure 14, *M. tuberosus* Hentz, should be considered a synonym of *M. interfector*, and this is in accordance with Chamberlin's opinion. Finally, the female shown in Figure 15, *M. syllepsicus* Hentz, belongs with the male of Figure 13. It is fortunate that the ample series of female *interfector* from Alabama clearly establishes the fact that *syllepsicus* is a synonym of *interfector*. In a later section I shall designate neotypes of each of these synonyms in order to clarify their position.

In the species of *Mimetus* treated below a record from Florida and another from a county in Georgia are included, since each of these areas is close enough to the boundary of Alabama to furnish additional evidence of distribution of the species.

Mimetus puritanus Chamberlin

Mimetus interfector Hentz (in part), Journ. Boston Soc. Nat. Hist., 6 : pl. 4, fig. 12. 1850.

Mimetus interfector Emerton (nec Hentz), Trans. Conn. Acad. Sci., 6 : 16, pl. 3, fig. 3. 1882.

Mimetus puritanus Chamberlin, Journ. Entomol. Zool., Pomona College, 15 : 3-6, figs. 1, 6. 1923.

Morphology. — The general ground color of both sexes is pale yellow or dirty white. The color of the folium on the dorsum of the abdomen of the female is quite solid, being plain brown or tinged with purple. The border of the folium is a serrated black line, and there are two comma-like pale or white marks between the shoulders. The caudal side of the shoulder humps may or may not have a white zone. The carapace is ornamented with thick brown or black double-Y-shaped lines, the apices of each Y reaching the ocular tubercles and the inner branches of the Y's joining behind the posterior median eyes. The right and left external zones of the carapace are each ornamented with a dot. The epigynum is broad caudally and unusually stout, and the aperture is visible from the ventral side. The outer margin of the cymbium of the male palpus has two spines located proximad of the apical one, a position not found in the other species.

Type locality. — Ithaca, Tompkins County, New York.

Distribution. — Alabama: Baldwin County, Dyas Creek, females; Dale County, Ariton, male; Morgan County, Cave Spring Cave, females. Georgia: Muscogee County, Upatoie Creek, female.

This species is distributed throughout the Appalachian Highlands. In Alabama it occurs only occasionally, and is present not merely in the Cumberland Plateau and the Piedmont, but also in the lower portion of the Coastal Plain. Both *puritanus* and a number of other spiders of known Appalachian distribution appear to have extended their ranges into the Coastal Plain from the Piedmont by way of the Chattahoochee and Pea river valley systems.

Ecology. — This species is found on the under surfaces of the leaves of gallberry (*Ilex glabra*), holly (*I. opaca*), and various other evergreen and deciduous shrubs. It has also been seen in impressions in the overhangs of ledges near the mouth of a cave. It occurs in ravines having hardwood and hardwood-coniferous cover, as well as in flat woods, particularly of the loblolly- and longleaf-pine types. It is not known from uplands. In one locality it was observed inside an old building. The information available in my field notes indicates that *puritanus* attacks two species, *Tidarren fordum* (Keyserling) and *Theridion tepidariorum* C. L. Koch.

Mimetus interfector Hentz

Mimetus interfector Hentz (in part), Journ. Boston Soc. Nat. Hist., 6 : pl. 4, fig. 13. 1850.

Mimetus tuberosus Hentz, *ibid.*, p. 3, pl. 4, fig. 14. Neotype, Alaga, Houston County, Alabama, male, August, 1940. Archer collection, Alabama Museum of Natural History.

Mimetus syllepsicus Hentz, *ibid.*, p. 34, pl. 4, fig. 15. Neotype, Randon's Creek, Monroe County, Alabama, female, April, 1940. Archer collection, Alabama Museum of Natural History.

Mimetus interfector, Chamberlin, Journ. Entomol. Zool., Pomona College, 15 : 3-7, figs. 5, 9. 1923.

Morphology. — The general ground color of both sexes is nearly white or, occasionally, faintly green. The folium on the dorsum of the abdomen of the female usually consists of a broad black disk beginning at the pedicel and extending back to the shoulders; from there it may or may not reach the apex. The folium of one female is in the form of an irregular mass of wavy broken lines and red spots. Its abdomen is broader proportionately than that of either *M. puritanus* or *M. notius*. The shoulder humps or horns are quite prominent, except in gravid females. The abdomen of the male is ovate, and the dorsal pattern is rather variable. In some males the pattern may consist of four large spots, but in other males the folium is marked by a series of irregular brown or black lines, and there may be a dis-

tinctly serrated border. One or more pairs of pale spots may also be present on the folium. The carapace of both sexes has a bifurcated black or brown line united anteriorly and posteriorly, usually with a longitudinal bar. The pattern of the female may be very broad and irregular in its posterior extension, and there are often a pair of black dots behind the posterior median eyes and a pair on the external lateral region of the carapace. The chelicera is black from the fang one third to more than one half the way back to the base. The labium has a pair of dots.

The epigynum is rather elongated, with the sides a little more parallel than they are in the other two species. The aperture is not visible from the ventral view. It is partly divided into a distal and a proximal portion by lateral processes. The cymbium of the palpus of the males terminates apically in a very prominent spine, and the apex of the bulb bears two lobes. The anal tubercle is small.

Type locality. — Male neoholotype and female allotype, Tuscaloosa, Tuscaloosa County, Alabama, October, 1938, January, 1939, Archer collection, Alabama Museum of Natural History. Hentz lived in Tuscaloosa from 1842 to 1846, and it may have been in this locality that he collected the male on which the species is based.

Distribution. — Alabama: Baldwin County, Jackson Oak, female, Magnolia Springs, male; Coosa County, Hatchet Creek, females (rather frequent); Houston County, Alaga, immature specimens, Omussee Creek, female; Jefferson County, Birmingham (R. V. Chamberlin); Monroe County, Randon's Creek, female; Shelby County, Morgan Station (R. V. Chamberlin); Tuscaloosa County, Alberta City, female, Tuscaloosa, females and males (frequent). Florida: Calhoun County, Bristol, females and males. This species is known from the southern two thirds of the state.

Ecology. — The spiders are found on the under surfaces of the leaves of holly, laurel (*Kalmia latifolia*), stinking bay (*Illicium floridanum*), bay (*Magnolia glauca*), and bull bay (*M. grandiflora*), hydrangea, and ironwood. In the winter it prefers evergreen shrubs, except when stalking its prey. It is also found under high hedges, and it invades the basements of houses. The preferred situations are hardwood, hardwood-coniferous ravine areas, and lowland woods. I have observed it preying on some of the following spiders: *Tidarren fordum* (Keyserling), *Theridion tepidariorum* C. L. Koch, *Metepeira labyrinthea* (Hentz), *Aranea miniata* (Walckenaer), *A. pegnia* (Wal-

ckenaer), and several species of *Dictyna*. Its egg sacs are roughly oblong and are fastened to the web of a theridiid or argiopid spider.

Mimetus notius Chamberlin

Mimetus notius Chamberlin, Journ. Entomol. Zool., Pomona College, 15 : 3–5, 7, figs. 4, 10. 1923.

Morphology. — The ground color of both sexes is pale yellow. The folium on the dorsum of the abdomen of the female is a mass of curved, wavy, or zigzag black lines, with some red markings interspersed, especially in the region of the shoulders. It is sometimes bordered by a deeply serrated line. A white mark is often present on each of the shoulders. The shoulder humps are very elevated in the females. In the male the pattern may be very much like that of the female or it may be merely a series of dots on a brown background. The carapace has a group of variously branching black lines. The anterior portion of the pattern is W-shaped, each apex terminating close to the ocular tubercles. The distal end of the chelicera is black, but the color does not extend far proximad; the rest of the chelicera is brown. It must be borne in mind that there are some exceptions to the patterns described above.

The epigynum is very wide at the base, rather short, and bluntly narrowed apically. The aperture resembles that of *interfector* in not being visible from the ventral view, but differs in not being armed with teeth. The cymbium of the male palpus is terminated by a short, wide curved spine, but the apex of the bulb bears only one lobe.

Type locality. — Runnymede, Osceola County, Florida, R. V. Chamberlin.

Distribution. — Alabama: Baldwin County, Bay Minette, females, Dyas Creek, females, Hog Creek, female; Cherokee County, May's Gulf, female; Cleburne County, Cheaha State Park, females; Covington County, Red Level, immature specimens; Escambia County, Brewton, female, Little River State Park, female; Geneva County, Panther Creek State Park, female; Hale County, Prairieville, females and male; Houston County, Dothan, females and male (frequent); Jefferson County, Cooley Creek, immature specimen; Lee County, Chewacla Creek State Park, females; Mobile County, Satsuma, female, Spring Hill, immature specimen, Mobile, female (H. P. Loding); Montgomery County, Waugh, female; Tuscaloosa

County, Tuscaloosa, female and male. This species has been found over most of the state except in the region of the Tennessee Valley.

Ecology. — This species is found on the under surface of the leaves of evergreen shrubs in swamp woods (red gum, tupelo), in ravine woods on laurel and huckleberry, and in upland woods (pine, blackjack oak, turkey oak) on yaupon (*Ilex vomitoria*), gallberry, and pin oak (*Quercus laurifolia*). It is present in longleaf-pine areas. On the whole, *M. notius* is not partial to any single habitat complex, and it is in dry upland country. It is quite common in red-cedar thickets on chalk prairies. It also invades buildings. I have noted it particularly in cabins in state parks and in tourist camps, as well as on picnic tables.

I have observed *M. notius* preying on some of the following species of spiders: *Theridion tepidariorum* C. L. Koch, *T. spirale* Emerton, *Latrodectus mactans* (Fabricius), *Tetragnatha laboriosa* Hentz, *Metepeira labyrinthea* (Hentz), *Aranea pegnia* (Walckenaer), and *Eustala anastera* (Walckenaer).

Mimetus tillandsiae, sp. nov.

Carapace elongate-cordate and having black spines, one posterior pair preceded by two sets of three spines, one spine behind PLE, one spine between PLE and PME, one pair between PME and AME. Carapace pearly, with ruddy margins. Legs and appendages waxy. Legs having the stout spines buff and the typical arrangement. Palps spinose. Sternum two thirds as wide as long. Coxae I and II close together; III and IV close; IV well separated from each other. Abdomen oval and lacking humps; scattered hairs present. Dorsum of abdomen with chalky lateral stripes and a central longitudinal stripe; two olivaceous stripes interposed, surmounted with hairs; bases of these hairs red; a basal black spot; a premedian lateral spot on each olivaceous stripe and followed by three similar spots in the apical region. Length 5.0 mm. Legs, 1 2 4 3 arrangement; I pair, femur 1.0 mm., tibia 3.9 mm., tarsus 4.0 mm., metatarsus 20 mm.

Epigynum as illustrated in Figure 1. Pit on dorsal surface not visible except in caudal view. Aperture having three denticles on caudal border, oval, and with a black border; no dorsal strip apparent. Caudal end of epigynum faintly indented toward the lateral borders. Spermathecae long, not noticeably constricted at the

isthmus, the anterior and caudal ends diverging. This species contrasts with *M. hesperus* Chamberlin in the internal structure of the epigynum and in having more nearly parallel sides. The abdomen is more nearly oval and the longitudinal markings contrast with the transverse black lines that occur in the few specimens of *M. hesperus* that I have seen.

Type Locality. — Female holotype, Allandale, Volusia County, Florida, December 30, 1940. Female immature, paratype, Jackson Oak, Baldwin County, Alabama, January 17, 1941. Archer collection, Alabama Museum of Natural History.

FIG. 1. *Mimetus tillandsiae.* Allandale, Volusia County, Florida

In both localities this species was taken in Spanish moss (*Tillandsia usneoides*) in hammock woods. It seems to prey on *Eustala anastera* (Walckenaer) and other species.

The seasonal distribution of Mimetus. Adult females and males of two of the four species in Alabama have a rather wide seasonal distribution. The seasonal data are as follows:

M. puritanus: June, ♀ ♂; July, ♀ ♂.
M. interfector: January, ♀ ♂; March, ♀; April, ♀; June, ♀; July, ♂; October, ♂; December, ♀.
M. notius: May, ♀ ♂; June, ♀; July, ♀; August, ♀; September, ♂; October, ♀ ♂; November, ♀.
M. tillandsiae: December, ♀.

ERO C. Koch, 1837

The genus *Ero* is represented by three known species in Alabama. Although it is very uncommon, enough specimens have been collected to indicate that it has a state-wide occurrence. In the Tennessee Valley it appears to be more widely represented than *Mimetus*. There is evidence that all three species construct some sort of web or shelter, but the web is very simple and small. I have no data on the prey of spiders of this genus, but on two occasions I found wandering individuals close to the web of species of *Lephthyphantes* (linyphiid spiders). Comstock[6] states that the egg sacs are nearly spherical and are suspended by a string of coarse threads which envelop them.

The female genitalia of *Ero canionis* Chamberlin and Ivie have never been described. Although this species is known only from the northern Appalachian Highlands and the Rocky Mountains, it seems advisable to include it with the Alabama species in the following key:

1. Epigynum a single prominent, bilobed, heavily chitinized mass; the vulva obscured by a lidlike projection; the surrounding area above the epigynum not clothed by long hairs ..... *Ero lodingi*
1. Epigynum not prominent, bilobed, or heavily chitinized; the area above the epigynum clothed by scattered hairs 2
2. Epigynum simple; spermathecae visible, not being obscured by chitinous plates 3
3. Spermathecae shaped like fishhooks, the short terminations facing each other, and less than a diameter apart; caudal margin of epigynum rimlike ..... *Ero canionis*
3. Two large circular holes, one diameter apart, on either side of a central plate; each extending into a diverging spermatheca ..... *Ero pensacolae*
2. Epigynum complex; having a small central plate, roughly kidney-shaped, deeply incised in the center; each lateral wing of the central plate bordered by a chitinous diagonally placed lappet . *Ero furcata leonina*

Ero furcata leonina (Hentz)

Theridion leoninum Hentz, Journ. Boston Soc. Nat. Hist., 4: 277, pl. 9, fig. 12. 1847.

Ero thoracica Emerton Trans. Conn. Acad. Sci., 4: 18, pl. 3, fig. 5. 1882.

Morphology. — This species has a pair of dorsal tubercles on the abdomen and resembles *E. canionis* in this respect and also in coloration. The American species has been considered identical with the European *Ero furcata* (Villers). Although there are no major dif-

[6] Comstock, J. H., *The Spider Book*, rev. and ed., W. J. Gertsch, p. 534. New York: Doubleday, Doran & Co., 1940.

ferences in the epigynum of the female and although the male palpus in both the American and the European specimens is nearly identical in most details, there are differences in the median apophysis. Emerton's figure of the palpus brings this out plainly. A comparison of specimens from Switzerland and North American males shows that in the former the median apophysis is prominent and single, whereas in American specimens it is blunt and bilobed. The differences do not seem to warrant specific separation, but indicate that the American form is a separate geographical race. Hentz's name is the first one available for it.

Type locality. — Male neoholotype and female allotype, Ramsey, Bergen County, New Jersey. W. J. Gertsch, collector, June 3, 1934. American Museum of Natural History, New York.

Distribution. — Alabama: Jackson County, Clear Creek, immature specimen; Lee County, Opelika, immature specimen; Madison County, Panther Knob, Monte Sano, female.

Ecology. — On dead leaves of the leaf carpet, slopes of hardwood ravines; on the under surface of a limestone slab in a rock pile at the end of a fissure on a mountain slope.

Ero lodingi, sp. nov.

Very close in appearance, size, and coloration to *E. furcata leonina* and *E. canionis*. Carapace having a longitudinal dusky line,

Fig. 2. *Ero lodingi.* Mobile, Mobile County, Alabama

not furcate; the line surmounted by a single anterior hair followed by two pairs of hairs. Area around eyes not dusky, but lateral sides of the widely cordate carapace bordered with black. Cervical pit deep. Base of the abdomen a mass of black splotches on deep gray, and with white fat bodies interspersed and visible through the cuticula; border of pigmented mass wavy. Apical half of abdomen light gray, with numerous white fat bodies visible; four horizontal lines

extending from the anus about halfway up the apical division, each line progressively wider. Legs having a series of blackish rings; femur, tibia, and tarsus three-banded; one band on the patella. Length 3.0 mm., length of first pair of legs 5.9 mm.

Epigynum as shown in Figure 2.

In external appearance this species differs markedly from all others in that the abdomen lacks tubercles.

Type locality. — Female holotype, Mobile, Mobile County, Alabama, January 16, 1941. Archer collection, Alabama Museum of Natural History.

The specimen was taken inside an overturned flower pot on the greenhouse property of H. P. Loding (urban area of Mobile).

Ero pensacolae Ivie and Barrows

Ero pensacolae Ivie and Barrows, Bull. Univ. Utah, 26 : No. 6, 19–20, pl. 7, fig. 54. 1935.

Morphology. — The color of this species is noticeably lighter than that of other North American species. Gray and white tones predominate. *E. pensacolae* is the smallest species of *Ero* described from North America. The largest Alabama female measures 2.4 mm. in length; the other species attain at least 3 mm. The first pair of legs are of considerable length, being about 5.7 mm. The most distinctive characteristic, however, is the presence of two pairs of tubercles on the dorsum of the abdomen; the other species either have one pair or lack them entirely. The epigynum is shown in Figure 3.

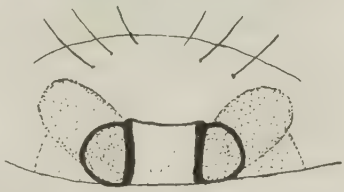

Fig. 3. *Ero pensacolae.* Cypress Creek, Lauderdale County, Alabama

Type locality. — Gainesville, Alachua County, Florida.

Distribution. — Alabama: Lauderdale County, Cypress Creek, female; Baldwin County, Gulf State Park, slightly immature male. Florida: Santa Rosa County, Pensacola, female (W. M. Barrows).

Ecology. — On the upper surfaces of partly curled dead leaves, hardwood ravines (oak), and hammock woods.

Alabama Museum of Natural History
University, Alabama

INDEPENDENT INHERITANCE OF CERTAIN CHARACTERS IN THE DEER MOUSE, *PEROMYSCUS MANICULATUS*

ELIZABETH BARTO

AS PART of a study to obtain additional information on the segregation of hereditary characters in the deer mouse, *Peromyscus maniculatus*, tests for linkage have been completed between the following pairs of traits: albino and dilute, albino and postjuvenal nude, albino and waltzing (*bairdii* type), hairless and dilute, hairless and ivory, and dilute and ivory. Each of these characters has been shown by other investigators to be inherited as a single-factor autosomal recessive. The albino form was reported by Sumner and Collins (1922), hairless by Sumner (1924), dilute and waltzing by Dice (1933, 1935), nude by Clark (1939), and ivory by Huestis (1938).

The albino and hairless mice used were descendants of animals of these types which were sent to the University of Michigan by Dr. F. B. Sumner in 1925. Ivory mice were kindly supplied by Dr. R. R. Huestis. Dilute, waltzing, and nude mice were obtained from the stocks which have been maintained at the University of Michigan, where these characters were first observed.

Each of the linkage tests has been made in the repulsion phase. All of the F_1 generation had the wild-type appearance which is expected if the characters are produced by genes at different loci. Testcrosses (F_1's $\times$ double recessives) were made for each pair of characters studied. Data obtained from the F_2 generation also are presented for those experiments in which four classes of phenotypes were produced. The symbols used to designate the genes tested are the ones proposed by Clark (1938).

Chi-square tests have been used to determine the significance of differences between observed and expected results. A departure from expectation is considered highly significant if, with one degree

of freedom, the chi-square is more than 6.635. This value marks the one per cent level of probability and is equivalent to a standard error 2.576 times as large as the deviation.

The formulas used to calculate chi-square are those listed by Mather (1938). Linkage relationships are shown by the joint segregation of the two pairs of genes being tested. The segregation of the single factors, however, determines the formula most appropriate for obtaining the chi-square for detection of linkage. The chi-square for single-factor segregations was determined, therefore, in each test by the formula

$$\chi^2 = \frac{(a_1 - la_2)^2}{ln},$$

where a_1 and a_2 are the observed numbers in the dominant and recessive classes, n is the total number of individuals, and $l : 1$ is the expected ratio. The same formula was employed for determining the chi-square for joint segregation in a testcross. In this case a_1 and a_2 represent the observed numbers of parental types and recombinations. The chi-square for detection of linkage in data from the F_2 generation was found from the formula

$$\chi^2 = \frac{(a_1 - 3a_2 - 3a_3 + 9a_4)^2}{9n},$$

where a_1 and a_4 are the numbers observed in the double-dominant and double-recessive classes, respectively, and a_2 and a_3, the observed frequencies in the two classes having one dominant and one recessive trait. For those experiments in which a significant disturbance of one of the single-factor segregations was found, the data are also presented in contingency tables from which the chi-square for detection of linkage is determined from the formula

$$\chi^2 = \frac{(a_1a_4 - a_2a_3)^2n}{(a_1 + a_2)(a_3 + a_4)(a_2 + a_4)(a_1 + a_3)}.$$

This formula is unaffected by anticipated single-factor ratios and, therefore, is better adapted for revealing linkage when one of the single-factor ratios differs significantly from the expectation.

I am indebted to Dr. Lee R. Dice for advice and criticism throughout the progress of the study and to Dr. C. W. Cotterman for suggestions concerning the statistical treatment of the data.

ALBINO AND DILUTE

Matings between albino (*cc DD*) and dilute (*CC dd*) mice had been made by Dr. F. H. Clark, and dilute individuals extracted from this cross in the F_2 generation were kindly turned over to me. Some of these mice proved to be heterozygous for albinism, and their use in producing the double recessives, which are phenotypically identical with *cc D* albinos, expedited this linkage test.

Albino mice are always clearly distinguishable from colored ones. The range of expression of the dilute character, however, extends from pale dilute, in which the hair tips are pale and the pigment in the basal half of the hairs is so much reduced as to appear white to the naked eye, to a condition indistinguishable from the wild-type even by microscopic examination. Thus of 548 offspring from matings of *dd* × *dd* mice 12 (2.19 per cent) failed to show the character. Unless the genes *c* and *d* are linked, therefore, a few more nondilute than dilute phenotypes would be expected in the testcross generation owing to inability to identify correctly all individuals homozygous for the dilute character.

As described by Dice (1933), the principal effect of the dilute character "is greatly to reduce the amount of black on the tips of the hairs." Clark (1938) reported dilute mice to be characterized by a reduction of black pigment both "in the tips of the hairs and proximal to the agouti bands." He also found lumps of pigment in the proximal portion of the hairs. Because some of the mice used in the testcross carried yellow genes, which also reduce the black pigment in the tips of the hairs, colored mice were classified as dilute or nondilute on the basis of the appearance of the proximal bands of their hairs. The same criterion was used for classification of the offspring from the crosses of *dd* × *dd* mice mentioned in the preceding paragraph. Microscopic examination for irregularities in pigment distribution in the bases of hairs plucked from the middorsum was made for individuals which could not be readily identified by macroscopic inspection. That the hairs might be long enough to show the character in *dd* genotypes, classification was made when the mice were twenty-four days of age or older.

Offspring from the testcross were divided among three phenotypes as follows: 66 colored nondilute, 61 dilute, and 110 albino mice (Table I). If the assumptions are made that animals in the three

TABLE I

ALBINO AND DILUTE

Testcross (*c D/C d* × *c d/c d*)

Class	*Observed*	*Expected*
Colored nondilute.....	66	60.55
Colored dilute	61	57.95
Albino	110	118.50
Total	237	237

ANALYSIS OF CHI-SQUARE

Source of variation	*Degrees of freedom*	*Chi-square*
Colored : albino ratio...	1	1.219
Linkage (colored nondilute : colored dilute ratio)	1	0.039

classes are equally viable, that no misclassification occurs, and that the genes are not linked, a 1 : 1 : 2 ratio would be expected. In other experiments, however, 2.19 per cent of the *dd* genotypes were assigned to the nondilute class. If it is assumed that the same amount of misclassification occurs in this experiment, the expected ratio is 70 nondilute : 67 dilute : 137 albino mice. A 1 : 1 ratio between colored and albino mice is expected, and the observed results closely approximate this distribution. Recombinations can be distinguished from parental types only in the two colored classes. Consequently, these two classes alone furnish information concerning the linkage relations between the genes *c* and *d*. If these genes are on different chromosomes, half of the 127 colored mice observed are expected to be *dd* genotypes, and half *Dd*. With the correction for misclassification of 2.19 per cent of the *dd* colored mice the expected frequency of the two phenotypes is 64.89 nondilute and 62.11 dilute. The chi-square for the nondilute : dilute ratio is then 0.039 for one degree of freedom. The deviation is not significant and, moreover, no excess occurs in the parental-type class. If the fiducial limit is set at 99 per cent the data would not fit a hypothesis of linkage with less than 39 per cent crossing over. The assumption can be made, therefore, that the genes *c* and *d* either are on different chromosomes or are only loosely linked.

ALBINO AND POSTJUVENAL NUDE

Postjuvenal nude (*nn*) mice can be distinguished from wild-type animals for a variable length of time. Clark (1939) reported that loss of hair in nude individuals began between the ages of two and three weeks and became complete when the mice were between twenty-five and thirty-five days old. He noted replacement of hair beginning when the mice were about fifty days old. Some adults with this character had a bare nose and tail; others were completely normal in appearance. In the present experiments, although some nude mice followed closely the schedule observed by Clark, others showed their abnormality for a shorter period. For example, two females were indistinguishable from normal mice at the age of thirty days, although seven days earlier they had been observed to be nude.

To obtain a better indication of the variability of the expression of this character, litters of seven matings between nude mice which had been observed to have conspicuous bare patches were examined at intervals of three days or less from the day of their birth until they were forty-four days old, and at intervals of four days or less between the ages of forty-five and fifty-one days. Examination of some of the litters was continued for a longer period. Since in each case both parents were nude, only *nn* genotypes were expected among the offspring. Of a total of twenty-three offspring from these matings three appeared normal at each examination. The deficiency of hair ranged in the others from slight thinning on the top of the head and on the posterior dorsum to total absence of hair except for the vibrissae. The earliest age at which the character could be recognized ranged from fourteen to twenty-seven days.

A bare spot was usually first noticeable in an area on the head between the ears and the eyes. As a rule the posterior dorsum next became bare. Hair was lost along the mid-dorsal line before the sides became nude. The order of progression varied, however. In some mice the posterior dorsum became bare before any baldness was apparent on the head; in others loss of hair proceeded continuously caudad along the dorsum from the eyes to the tail. Except for its proximal quarter inch the tail sometimes did not become bare until after the new pelage had been acquired on the rest of the body. In many specimens the region in front of the eyes, the sides of the

face, and the chin never became bare, even in mice which showed the character to a high degree.

The earliest age at which hair of the next pelage appeared was thirty days and the latest was forty-seven days. The interval between the time that loss of hair was apparent and the date on which incoming hairs were first seen ranged from eleven to twenty days. The bare areas, colorless when they first appeared, were suffused with black pigment from one to eleven days before the tips of the hairs of the next pelage became visible. Hair usually appeared first on the rump or saddle. Sometimes the head was the first area on which hair was replaced, but more often it remained bald until the rest of the pelage was practically complete. In all cases in which the base of the tail became bare it was the last part to regain its normal appearance. Of the twenty mice in this group which expressed the postjuvenal nude character one appeared normal at thirty-eight days of age. Four mice were characterized by a bare tail base at fifty-one days of age, when they were last examined. Three in which the pelage had been completely regained at the ages of thirty-seven, thirty-eight, and forty-six days again acquired bare areas, so that at the age of fifty days they could once more be recognized as nude animals.

In the F_2 and testcross generations from the cross of nude (*CC nn*) $\times$ albino (*cc NN*) mice all offspring classified as normal were examined at least once between the ages of twenty and thirty-seven days, with the following exceptions: three of the F_2 generation were classified at the age of forty days and two testcross offspring at forty-two days of age. Inasmuch as some *nn* genotypes do not differ in appearance from animals of the genotype *N*, a deficiency in the nude classes would be expected.

The F_2 generation was made up of 184 wild-type mice, 67 albinos, 33 colored nudes, and 16 albino nudes. The testcross offspring consisted of 108 wild-type, 102 albino, 51 nude, and 51 albino nude mice (Table II). This distribution differs noticeably from the 9 : 3 : 3 : 1 and 1 : 1 : 1 : 1 ratios expected if the characters are not linked and if all types are equally viable and can be reliably classified. An analysis of chi-square shows that the discrepancy between observed and expected numbers is due principally to the deficiency in the nude classes. The chi-square for the nonnude : nude ratio with one degree of freedom is 12.018 for the F_2 generation and 37.385 for the testcross.

TABLE II

ALBINO AND POSTJUVENAL NUDE

Class	F_2 ($C\ n/c\ N \times C\ n/c\ N$)		Testcross ($C\ n/c\ N) \times (c\ n/c\ n$)	
	Observed	Expected	Observed	Expected
Wild-type	184	168.75	108	78
Albino	67	56.25	102	78
Nude	33	56.25	51	78
Albino nude	16	18.75	51	78
Total	300	300	312	312

ANALYSIS OF CHI-SQUARE

Source of variation	Degrees of freedom	Chi-square	
		F_2	Testcross
Colored : albino ratio	1	1.138	0.115
Nonnude : nude ratio	1	12.018	37.385
Linkage	1	0.290	0.115
Total	3	13.446	37.615

These deviations are probably due largely to inability to identify all the *nn* genotypes. No significant departure from expectation is shown for the segregation of colored and albino types or for the joint segregation of the four traits. The chi-square for joint segregation, calculated from the data as set up in contingency tables (Tables III–IV), is 0.719 for one degree of freedom for the F_2 generation and 0.056 for one degree of freedom for the testcross. Neither value shows a significant departure from the results expected if the genes segregate independently. Furthermore, the deviations are in the direction opposite to that which would be produced by linkage.

ALBINO AND WALTZING

The waltzing character (*v-1 v-1*) tested for linkage with albinism arose in a stock of *P. m. bairdii* from Alexander, Iowa, and has been shown by Dice (1935) and Watson (1939) to be produced by a pair of genes at a different locus from that which controls waltzing be-

TABLE III

ALBINO AND NUDE

F_2 ($c\,N/C\,n$) × ($c\,N/C\,n$)

Chi-square for joint segregation = 0.719 for one degree of freedom

	Colored	Albino	Total
Nonnude.....	184	67	251
Nude.....	33	16	49
Total.....	217	83	300

TABLE IV

ALBINO AND NUDE

Testcross ($c\,N/C\,n$) × ($c\,n/c\,n$)

Chi-square for joint segregation = 0.056 for one degree of freedom

	Colored	Albino	Total
Nonnude.....	108	102	210
Nude.....	51	51	102
Total.....	159	153	312

havior exhibited in a stock of *P. m. artemisiae* from Lyon's Ferry, Washington. Dice reported variation in the degree of reaction of different mice and differences in the behavior of the same mouse on different days. Both he and Watson found that matings between waltzers produced a small proportion of offspring which did not express the character, and that deficiencies in the waltzing class were greater after outerosses than when matings were made only between animals of the Alexander stock.

The study of the linkage relationship between albinism and the *bairdii* type of waltzing was initiated by Dr. Margaret Liebe Watson. She crossed waltzers with albino hairless mice and obtained a number of animals in the F_1 and F_2 generations. Additional matings after she left the University of Michigan increased the size of these generations. Hairless waltzers have not yet been obtained in sufficient

TABLE V

ALBINO AND WALTZING (*BAIRDII* TYPE)

Class	F_2 (*C v-1/c V-1*) × (*C v-1/c V-1*)		Testcross (*C v-1/c V-1*) × (*c v-1/c v-1*)	
	Observed	Expected	Observed	Expected
Colored nonwaltzers	89	77.625	56	51.75
Albino nonwaltzers	28	25.875	58	51.75
Colored waltzers	15	25.875	44	51.75
Albino waltzers	6	8.625	49	51.75
Total	138	138	207	207

ANALYSIS OF CHI-SQUARE

Source of variation	Degrees of freedom	Chi-square	
		F_2	Testcross
Colored : albino ratio	1	0.010	0.237
Nonwaltzer : waltzer ratio	1	7.043	2.130
Linkage	1	0.158	0.043
Total	3	7.211	2.410

numbers to test adequately the linkage relationships between these two characters, and therefore only the data which concern the inheritance of waltzing and albinism are presented here. At the age of one month mice were tested for waltzing with the key-jingling apparatus described by Watson (1939). All mice classified as nonwaltzers were tested again at the ages of two and three months.

Of a total of 138 F_2 individuals 89 were colored nonwaltzers, 28 were albinos, 15 were colored waltzers, and 6 were albino waltzers (Table V). Fewer than one fourth of the mice are included in the two classes of waltzers. The chi-square for the segregation of nonwaltzing and waltzing types is 7.043, which indicates a significant deviation from the 3 : 1 ratio expected if waltzers and nonwaltzers are equally viable and if *v-1 v-1* genotypes always express the waltzing character. Since, however, it is known that some *v-1 v-1* mice show only normal behavior with the testing apparatus used in this experi-

TABLE VI

ALBINO AND WALTZING (*BAIRDII* TYPE)

F_2 (*c V-1/C v-1*) × (*c V-1/C v-1*)

Chi-square for joint segregation = 0.206 for one degree of freedom

	Colored	Albino	Total
Nonwaltzers	89	28	117
Waltzers	15	6	21
Total	104	34	138

ment, the shortage of waltzers is not surprising. Because of the significant deficiency of waltzers the chi-square for linkage was determined from a contingency table (Table VI). That the difference between observed and expected numbers is not due to linkage is indicated by the low value (0.206 for one degree of freedom) of this chi-square.

As one means of obtaining albino waltzers gray waltzers of the F_2 generation were mated together or to F_1 individuals. If waltzing and albinism are inherited independently two thirds of the F_2 colored waltzers would be expected to be heterozygous for albinism. If the two characters are closely linked the proportion carrying the gene for albinism would be expected to be smaller. Of five gray waltzers tested four had some albino offspring. The evidence from these matings, therefore, also indicates that the two characters are inherited independently.

From the testcross were produced 56 gray nonwaltzers, 58 albino nonwaltzers, 14 gray waltzers, and 19 albino waltzers (Table V). The analysis of chi-square shows no significant departure from expected numbers in this generation. For the ratio between parental types and recombinations the chi-square for one degree of freedom is only 0.0435, a value which indicates very close correspondence between the observed results and the 1 : 1 ratio expected if the genes *c* and *v-1* are not linked.

King and Castle (1937) found that in the rat (*Rattus norvegicus*) the genes for waltzing are linked to those for albinism with a crossover value of 45.8 ± 0.7 per cent. No indication of linkage be-

tween albinism and the *bairdii* type of waltzing was found in the deer mouse. In both the F_2 and the testcross generations the deviations from expectation were in the direction opposite to that which would be produced by linkage. Nevertheless not enough animals were reared in these tests to disprove a hypothesis of linkage with as much as forty-five per cent crossing over. If only deviations 2.576 times the standard error are considered highly significant, the data from the testcross would show highly significant departures from expectation only for crossover values of less than 41.77 or more than 59.68 per cent ($\rho \pm 2.576\ S_\rho$, where ρ is the observed proportion of the recombination types and S_ρ is the standard error of this proportion). If the genes for these two characters are not linked in the deer mouse it is probable that either the genes for albinism or those for the types of waltzing tested, or both, are not homologous in the two species. Clark (1936) has shown that in the deer mouse the gene for albinism is linked to the gene for pink-eye, which produces a phenotypic effect similar to the character of the same name in the rat and the house mouse, and that the crossover value is approximately the same in the deer mouse as in the other two species. Hence there is evidence that the genes for albinism in the deer mouse and in the rat are homologous. In view of the facts that at least two types of waltzing are known in the deer mouse and that these are known to be produced by different hereditary factors, it would not be surprising if the gene for the *bairdii* type of waltzing is not homologous with the one for the waltzing character studied in the rat.

HAIRLESS AND DILUTE

The age of hairless (*hr hr*) mice when their character first becomes noticeable varies considerably. Sumner (1924) observed that loss of hair began at the age of two to three weeeks. Of the hairless mice obtained in the F_2 and testcross generations following a hairless (*hr hr DD*) × dilute (*Hr Hr dd*) cross one had lost all its hair except the vibrissae by the age of nineteen days; others which appeared normal at twenty-seven days of age later lost their hair. Mice from these crosses were never assigned to the nonhairless classes until they were at least twenty days old. In most cases they were examined for hairlessness when they were thirty or more days old. Unless the pelage appeared light dilute by macroscopic examination hair samples were inspected with the microscope for the presence of

TABLE VII

HAIRLESS AND DILUTE

Class	F_2 (*Hr d/hr D*) × (*Hr d/hr D*)		Testcross (*Hr d/hr D*) × (*hr d/hr d*)	
	Observed	Expected	Observed	Expected
Wild-type	225	207.5625	59	47
Dilute	59	69.1875	39	47
Hairless	75	69.1875	58	47
Dilute-hairless	10	23.0625	32	47
Total	369	369	188	188

ANALYSIS OF CHI-SQUARE

Source of variation	Degrees of freedom	Chi-square	
		F_2	Testcross
Nondilute : dilute ratio	1	7.813	11.255
Nonhairless : hairless ratio	1	0.760	0.340
Linkage	1	2.279	0.191
Total	3	10.852	11.786

diagnostic lumps of pigment. For hairless mice this examination was made when the loss of hair was first noted. Other individuals were examined for dilution when they were classified as nonhairless. Since in animals which develop the character only to a slight degree the irregularities in pigment distribution are confined to the most proximal parts of the hairs, it is possible that in some *hr hr dd* mice the early loss of hair may have prevented the expression of the dilute character.

The F_2 and testcross generations included, besides the four expected classes, some albino and albino hairless offspring. These were produced from matings in which the ancestry of each parent included some albinos from which an albino gene could have been inherited. It is therefore assumed that each of these parents was heterozygous for *c* as well as for *hr* and *d* genes. Since albinos could not be classified by inspection as dilute or nondilute, they are not included in the numerical list of the types observed. Inasmuch as

TABLE VIII

HAIRLESS AND DILUTE

F_2 (*Hr d/hr D*) × (*Hr d/hr D*)

Chi-square for joint segregation = 3.493 for one degree of freedom

	Nonhairless	Hairless	Total
Nondilute.....	225	75	300
Dilute.....	59	10	69
Total.....	284	85	369

TABLE IX

HAIRLESS AND DILUTE

Testcross (*Hr d/hr D*) × (*hr d/hr d*)

Chi-square for joint segregation = 0.359 for one degree of freedom

	Nonhairless	Hairless	Total
Nondilute.....	59	58	117
Dilute.....	39	32	71
Total.....	98	90	188

independent inheritance has been demonstrated between albinism and hairlessness (Sumner, 1924, 1932; Feldman, 1937; Clark, 1938) and between albinism and dilute, disregard of the albinos should not change the proportions in the four expected classes.

Colored individuals in the F_2 generation were distributed as follows: 225 wild-type, 59 dilute, 75 hairless, and 10 dilute-hairless. The testcross included 59 wild-type, 39 dilute, 58 hairless, and 32 dilute-hairless mice (Table VII). Significant deviations from 3 : 1 and 1 : 1 ratios for nondilute and dilute mice are indicated in the F_2 and testcross generations by chi-squares of 7.813 and 11.255, respectively, for one degree of freedom. This deficiency may be due to the failure of some *dd* mice to be distinguished from nondilute animals. Because of the disturbance of the segregation between dilute and nondilute types chi-squares to detect linkage have been

calculated from contingency tables for the F_2 (Table VIII) and testcross (Table IX) data. For the F_2 the chi-square is 3.493 for one degree of freedom, and for the testcross it is 0.359. Departures from the expected joint segregation are not significant. The data can be explained, therefore, by assuming the characters dilute and hairless to be inherited independently.

HAIRLESS AND IVORY

The F_2 generation from a hairless (*hr hr II*) × ivory (*Hr Hr ii*) cross included 252 normal, 67 hairless, 79 ivory, 20 hairless-ivory,

TABLE X

HAIRLESS AND IVORY

Class	F_2 (*Hr i/hr I*) × (*Hr i/hr I*)		Testcross (*Hr i/hr I*) × (*hr i/hr i*)	
	Observed	Expected	Observed	Expected
Wild-type	252	235.125	97	81.25
Hairless	67	78.375	72	81.25
Ivory	79	78.375	84	81.25
Hairless ivory	20	26.125	72	81.25
Total	418	418	325	325

ANALYSIS OF CHI-SQUARE

Source of variation	Degrees of freedom	Chi-square	
		F_2	Testcross
Nonhairless : hairless ratio	1	3.907	4.212
Nonivory : ivory ratio	1	0.386	0.520
Linkage	1	0.010	0.520
Total	3	4.303	5.252

and 1 albino (Table X). Both parents of the albino mouse had albinos among their ancestors, and its occurrence can therefore be explained by assuming the parents to be heterozygous for this character. From the testcross were produced 97 normal, 72 hairless, 84 ivory, and 72 hairless-ivory mice. Mice were classified when they were twenty-four days of age or older.

The results obtained in the F_2 and testcross do not differ significantly from the 9 : 3 : 3 : 1 ratio expected if the characters are not linked. Highly significant departures from expected proportions are not observed in either of the single-factor ratios or in the joint segregation of both pairs of genes. The results therefore indicate that the characters either are not linked or, at least, are not closely linked.

DILUTE AND IVORY

The first matings designed to determine the linkage relations between ivory and dilute were made at the Cranbrook Institute of Science, which provided laboratory care of the animals and facilities for initiating this experiment. Before the test had been completed the stocks were transferred to the University of Michigan, where the work was continued.

Ivory (*D ii*) and dilute-ivory (*dd ii*) mice do not differ in appearance, and the expected proportions in the testcross if the genes are not linked are therefore 1 wild-type : 1 dilute : 2 ivory.

Because some of the dilute and ivory mice which were crossed were heterozygous for other mutant genes, many yellow and dilute-yellow, 4 albino, 3 pink-eye, and 4 cinnamon animals were produced in the testcross generation. Yellow mice were readily separable into dilute and nondilute classes, and their presence caused no difficulty in classification. The pale shade of the bases of the hairs of cinnamon and pink-eye mice makes the distinction between dilute and nondilute types difficult. It has been possible, however, by microscopic examination, to identify the dilute variation in some pink-eye and cinnamon mice, and data from matings which furnished these types are included in the tabulations. The colored offspring from matings which produced some albinos are also included in the frequency distribution.

One of the testcross matings has yielded twenty-eight offspring, all of which have normal-colored pelage. Eight of these mice resembled postjuvenal nude animals in having large temporary bare areas after the juvenile pelage had been lost. A similar absence of hair was noted in the F_2 generation in three mice from a mating which also produced forty-two offspring with the normal amount of hair. The parents of the temporarily bald mice were all descendants of the same dilute × ivory mating. None of them were related to any postjuvenal nude mice of the *osgoodi* type described by Clark (1939).

The deficiency of hair in these animals is being studied to determine whether the character is inherited, and it is hoped that information may be obtained which will explain the failure of either dilute or ivory mice to appear among the twenty-eight offspring from this one testcross mating. Only one fourth of the mice in the testcross generation are expected to have pelage of wild-type color. The probability that all the mice from this mating, by chance distribution of genes, would be of this type is therefore only $(\frac{1}{4})^{28}$. Since the wild-type color would be produced by a recombination of genes, any linkage between the *d* and the *i* genes would tend to reduce,

TABLE XI

DILUTE AND IVORY

Testcross $(D\ i/d\ I) \times (d\ i/d\ i)$

Class	*Observed*	*Expected*
Nondilute, nonivory	91	87
Dilute	89	87
Ivory	168	174
Total	348	348

ANALYSIS OF CHI-SQUARE

Source of variation	*Degrees of freedom*	*Chi-square*
Nonivory : ivory ratio	1	0.414
Linkage (nondilute, nonivory : dilute ratio)	1	0.011

rather than to increase, the proportion of mice in this group. The distribution of offspring from this mating is therefore even less in accord with a hypothesis of linkage than with an assumption of random segregation of the genes *d* and *i*. The results of this one mating are decidedly different from those of other testcross matings and, if added to them, would tend to conceal any indication of linkage if it does exist. They are therefore not included in the tabulation of the testcross data.

From the testcross matings which produced some albinos 7 nondilute, 6 dilute, and 11 ivory mice were also obtained. The litters of the testcross generation which included pink-eye and cinnamon animals consisted of 13 nondilute, 12 dilute, and 22 ivory specimens.

The other matings of the testcross produced 71 nondilute, 71 dilute, and 135 ivory individuals. The combined data (Table XI) from these three groups of matings show that 91 nondilute, 89 dilute, and 168 ivory mice resulted. The observed results are very close to a 1 : 1 : 2 ratio. Recombinations can be observed only in the nonivory mice. The chi-square for the ratio between the nondilute, nonivory mice and the dilute mice is 0.414 for one degree of freedom and indicates a very close agreement with the 1 : 1 ratio expected without linkage.

DISCUSSION

Cross (1938) counted forty-eight chromosomes in each of these species: *P. m. gambelii*, *osgoodi*, *bairdii*, *artemisiae*, *sonoriensis*, and *blandus*. The number in *P. m. hollisteri* he found to be fifty-two. The mice used in the present study were hybrids between different subspecies, including *P. m. gambelii*, *osgoodi*, *bairdii*, and *blandus*. *P. m. hollisteri* was not represented in any of the stocks employed. It seems probable, therefore, that the mice on which linkage tests were made had twenty-four pairs of chromosomes, although no counts were taken for any of these individuals. The purpose of the linkage studies has been to discover linkage groups and to determine markers for the different chromosomes.

The only linkage group known in *Peromyscus* includes the characters albino and pink-eye and has been designated Number I by Castle (1940). These characters were shown by Sumner (1922, 1932) to be linked. Clark (1936) demonstrated that the degree of linkage between them is approximately the same as that observed between albinism and pink-eye in the house mouse and Norway rat, which are included in linkage Group I of these two species. His final determination (1938) of the amount of crossing over between the two genes in the deer mouse gave a value of 19.94 ± 1.44 per cent in females and 13.16 ± 2.70 per cent in males.

Two other chromosomes in *Peromyscus* have been previously marked by yellow and hairless. Sumner (1922), Feldman (1937), and Clark (1938) showed that albino and yellow are independently inherited. Random segregation of albino and hairless was demonstrated by Sumner (1924, 1932), Feldman (1937), and Clark (1938); and yellow and hairless showed no linkage in the experiments of Feldman (1937) and Clark (1938).

The present study completes the evidence necessary to establish dilute as a marker for a fourth chromosome. Clark (1938) found that dilute is not linked with yellow, and independent inheritance has been shown here between dilute and albino and between dilute and hairless.

Four of the chromosomes, therefore, can now be designated by genes located upon them, as follows: the albino chromosome, the yellow chromosome, the hairless chromosome, and the dilute chromosome.

Independent inheritance of a number of other pairs of characters has been shown by other investigators (Feldman, 1937; Clark, 1938; Huestis, 1940) and by the present report, but no trait has yet been tested for linkage with markers for all four of the chromosomes listed above. Studies now in progress are designed to discover additional linkage groups or markers for the remaining twenty pairs of chromosomes.

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MATING OF THE GARTER SNAKE *THAMNOPHIS SIRTALIS SIRTALIS* (LINNAEUS) *

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A GENETICAL study begun in 1922 has branched out into a general life-history record of the garter snake *Thamnophis sirtalis sirtalis*. In the earlier years of the work the genetical aspect predominated and other observations were incidental; the desired matings were obtained, but the process of mating was disregarded. At that time only a few snakes were in use, and the male and female wintered together, so that only by chance was copulation seen in the spring. But since 1932 the males have been segregated throughout the year, and only for the hour (more or less) required for courtship and copulation has a male been in the pit of a female. At the earliest opportunity in spring the chosen male is, under this arrangement, dropped into the pit housing the female, perhaps with other females. In order to know that the scheduled mating, and no other, occurs, it is of course necessary to watch the snakes carefully until the male is removed from the pit. The routine, therefore, has not only given an excellent chance to observe mating behavior, but has necessitated observation of it.

One not familiar with this behavior of the garter snakes may easily misinterpret it, erroneously assuming copulation when the snakes are merely in the position in which it might take place. It seems obvious in a paper by D. Dwight Davis [1] that this mistake has

* Contribution from the Department of Zoölogy, and Paper No. 779 from the Botanical Gardens and Department of Botany, of the University of Michigan.

† Most of the data on which this paper is based were gathered during the period when the authors worked together, from 1922 to 1937 (the year of Dr. Blanchard's death), but a few additional records were made in the two subsequent springs. For the manner of handling the data and the wording of the paper I am responsible. F. C. B.

[1] "Courtship and Mating Behavior in Snakes," *Zool. Ser. Field Mus. Nat. Hist.*, 20 (22) : 257–290. 1936.

been made throughout the description of courtship and mating in *Thamnophis radix*, and that at no time during the observations did mating occur. The fact that such a mistake can so easily be made and accepted prompted this report of mating as it has repeatedly been seen in the pits, where the snakes, though captive, are under the fairly natural conditions set forth in an earlier paper.[2] No single instance is related in detail, but recorded data are summarized and a description given of typical behavior based on about fourscore instances. Usually two observers working together have watched several pits at once, and in this way nearly a hundred copulations and many abortive courtships have been witnessed.

THE TIME OF MATING

In very early spring, when the sunshine first brings out the snakes, their mating activity seems to depend on the weather alone. A warm sunny day starts courtship, and, if conditions are good enough, copulation follows. Though a record of temperature was not always kept we soon could recognize the right weather and learned not to waste time trying to work with the snakes unless the sun was shining and the air temperature above 60° F.

In the pits the usual mating season is from early April to early May, the later half of April being the time when our work has been most profitable. But matings have been secured in a warm spell in March, and as late as May 11. In the sixty-three matings of the years 1932 37 inclusive, the dates ranged from April 4 to May 4, except for four matings which were unusually early, on March 16 and 22, and three which were very late, on May 11. These extremes agree with those in nature, if we may judge from the meager field evidence at hand; but there are probably more of the early matings in nature than in the pits, for to conserve our time we let pass unused some questionably suitable days of which the wild snakes may have availed themselves.

But later in the spring the weather of the day is not the only factor to be considered. After a number of suitable days have passed the snakes, though still not mated, seem to lose the necessary impulse and become indifferent to each other. For this reason

[2] Factors Determining Time of Birth in the Garter Snake *Thamnophis sirtalis sirtalis* (Linnaeus), *Pap. Mich. Acad. Sci., Arts, and Letters*, 26 (1940 : 161 176. 1941.

many attempts to bring about copulation in May have failed, though the weather was perfect. The female is first to lack response, the male sometimes working for an hour or more before she is finally induced to copulate, and sometimes failing altogether. Early in May he, too, becomes languid in courtship until, at length, chancing to find a female, he shows no interest in her. Thus, in early spring (March and April) the weather of the day seems to be the determining factor in courtship and mating, whereas in late spring (very late April and May), when the weather is more uniformly suitable, it is the date (that is, the length of time since warm weather started) that apparently controls the activity. After the beginning of May one is lucky to secure mating.

In late summer there seems to be a reversal of this condition. Apparently there is no courtship in early summer, even on cool springlike days; but in August, when the broods are appearing, the males again pay some slight attention to the females, though their courtship is such as hardly to deserve the name. In Indian summer a bright warm day after early cool weather induces real courtship, which may even lead to copulation. Thus, after a certain date, suitable weather is all-important again.

The actual dates of copulations recorded in this paper have no significance other than that they were within the mating season, were suitably warm and sunny days, and were for us free of more urgent work.

COURTSHIP AND COPULATION

Transference of the male from his own pit to that of the female seems not to frighten him, and his abrupt arrival from above usually disturbs the female but little, if at all. The male at once begins a slow exploration of the unfamiliar pit, with much action of his tongue. Perhaps he recognizes the presence of a female and actually seeks her, but this seems doubtful, for, once he has accidentally stumbled upon her, his search when she eludes him is a very much more active hunt. When touched by the male the female may continue to lie quietly as before or may glide away a few feet, quickly, sometimes with vibrations of the tip of her tail.

As soon as the male happens to touch the female, if weather, temperature, and time of season are appropriate, there is no doubt of his interest. Exploration of the pit is abandoned. If she has not

darted away he noses (or, rather, "chins") his way rapidly along her back, usually but not always starting first toward the region of her vent, then turning and retracing his course forward again along her back until their tails lie close together, his body lying upon hers (or in part beside hers) with enough slack to keep the same general position. Usually the male is so much smaller that his head is far behind the female's. Often he chins too far forward and must gain the needed position by backing. Even if she is somewhat coiled his body seldom takes short cuts, but lies draped along hers, waved from side to side enough to maintain the superior posture. No part of his body encircles hers, though a part of it sometimes curves down to beneath hers and up again on the same side; and his vent region repeatedly loops well down near her vent. His tail is often twisted under hers, wedging it up from the ground for a few seconds, and, in a strenuous courtship, often a part of his body, beneath hers, throws it up from the ground repeatedly.

Though there may be several females in a group, and though the male may temporarily lose touch with the one he has started to court, he usually finds the original female again and persists with that one exclusively, ignoring the others. In a group of females he may become temporarily confused, his tail working actively about the tail of one female, his body rippling over the body of another in the group; but shortly he becomes oriented. If the female moves away he follows her, leaving the others, even gliding over them, without hesitation. This is so usual as to justify the statement that snakes have individuality to one another — unless perhaps the male recognizes his own scent on the female after having touched her, which seems less likely.

The male proceeds regardless of the similar activity of other males with the same female, apparently either oblivious to or possibly urged on by it, certainly not discouraged. When two or more males simultaneously court a female each is apparently as energetic or as languid as he would be were the others not present. There is certainly no evidence of deference by any male to priority or superiority of another. True, one male often seems to delay while another courts actively; but he will show no more zeal if isolated with an unattended female. This is his individual reaction. Because of the great difference in the vigor of different males, especially when the season for mating is not at its height or the weather conditions not

near the optimum, one must be cautious in suggesting that a male recognizes the dominance of his rival and so postpones courtship. We have not seen any evidence of such forbearance.

Possibly courtship by a male is intensified by the presence or similar activity of another male, though this, too, seems doubtful. Certainly the presence of another male is not necessary for courtship at its highest intensity. Several active males, each struggling for the position necessary for copulation, push one another from the female, but this seems to be done incidentally, not purposefully. Apparently each male merely strives to attain and maintain the position, not to dislodge a rival.

During the courtship the male is so intent as to be careless of disturbance; the female, however, retains her usual vigilance and is perhaps more than ordinarily alert.

As soon as the male attains the mating position on the female, which is usually accomplished in a few seconds, his tail and posterior body feel continuously about hers in an exploratory manner, and convulsive waves within his body roll forward rhythmically. It is hard to describe this motion, even while watching it; one can only say that a series of ripples or undulations within the body run forward from the tail, followed, after a pause of a few seconds, by another series of ripples. It would seem that these might be a stimulation either to the female or to the male himself. The contractions do not alter his position on the female. From time to time, if copulation does not occur quickly, he begins all over again, turning and nosing down her body to the tail region, his chin in contact with her back, rapidly reversing and coming forward again to take up the old position, the manipulations with the tail, and the internal waves. This repeats the maneuver following his first finding her, and would seem to be for reassurance. It may be repeated many times in a slow courtship. He may even wander off a little way and come back again to her, though this is unusual if the conditions are favorable.

Several times attachment within two or three minutes has been seen, and once within a minute; but at least five or ten minutes of courtship has been more usual, and often, even with great energy on the male's part and perfect weather, the attachment has been accomplished only after half an hour or even an hour. If the season and the weather are at their best, however, the preliminaries will be more brief.

Sometimes the male shows enough interest to take up the position along the female, but does little more, merely lying so in the sunshine. Courtship unconsummated is common when either the temperature or the time of year is unsuitable. In early spring, when the weather, though sunny, is still too cold, the male takes the position of courtship, with more or less of its activity depending on how nearly suitable the conditions are; as the conditions are relatively more favorable the male is more active. But the preparatory maneuvers have often been seen to go on more or less vigorously for an hour or longer and then wane without copulation, the male finally wandering off. Later, when the weather is perfect but the season too advanced and the females grown unresponsive, the males still continue courtship — for a time energetically, but gradually, as the days pass, with less and less vigor, until finally there is a period of mutual indifference. This activity must not be interpreted as copulation, and the position of the male looping down at the female's vent must not be assumed to mean attachment. In fact, that position indicates that attachment has *not* occurred.

The act of copulation takes place suddenly and with a maneuver of the tails too quick to follow with the eye. Apparently the raising of the female tail to a nearly vertical position is involved, but whether or not in part by the female herself is a question. It seems as though the male in one of those upward wedgings of the female's tail with his suddenly throws it straight up. There is a flash of motion of the pair, and then stillness. The male usually relaxes and slides off the female just as soon as the hemipenis has been inserted, the vent being the only point of contact remaining. As long as there is agitation, and the male holds his position over the female, it is safe to guess that there is no attachment; when attachment occurs no guessing is necessary, for it is made plainly visible by separation of the bodies except at that point, generally with enough tension to expose a rim of the soft internal tissues.

After the paroxysm of attachment the female usually begins to glide very slowly away, dragging the male, who is carried along with only slight effort on his part. The position of the male's body in relation to the female's shows which hemipenis is in use. He may head in the same general direction as the female and contribute somewhat to the motion, or simply be pulled backwards. They may settle down again or continue to move very slowly, but

during the time of attachment they do not move quickly if undisturbed. Only rarely does the male repeat, and then in a sluggish manner, the glide up the back of the female. The waves of contraction which rippled up the body of the male usually stop entirely at copulation, so apparently are not a part of insemination. Though there may be some irregular movements, the quick energetic rhythm, characteristic of precopulation, very rarely occurs.

The usual duration of the attachment has been found to be about fifteen to twenty minutes, but has varied from five to thirty minutes. There is some evidence that insemination is not immediate, or at least not quickly completed, in that unusually short copulations have not given young. At completion the hemipenis is reverted, not withdrawn; the pair quietly drop apart, and neither snake has any further interest in the other. Though the male may promptly mate again, with another female, he shows no more interest in this one. Only once, and that when a disturbance caused premature separation, has there been seen any further attempt by the male to resume mating with the same female after detachment. But if the male finds another female he may at once repeat the whole act, and he may even complete a third successful copulation resulting in young. The female, though, having once mated, seems intolerant of any further courtship, at least for some time.

MISINTERPRETATION OF THE COURTSHIP POSITION

Frequently snakes seen in active courtship, or even lying quietly in the position taken in courtship, have confidently been reported as mating, or in copulation. This mistake is perhaps natural. But because of the vital difference between the two acts, and the fact that false genetical and physiological conclusions may result from confusing them, it has been thought worth while to emphasize here the differences in the two behaviors.

The apparent discrepancies between this paper and that by Davis (*op. cit.*) are thought to result from such a misinterpretation, rather than from differences between the two species of garter snakes (*Thamnophis sirtalis* and *T. radix*), which are so alike that it would be rather surprising to find a great variance in their breeding behavior. The few casual observations of *T. radix* in our pits are in accordance, so far as they go, with those of *T. sirtalis;* though the species has not been seen in copulation, it has been witnessed in a

courtship like that of *T. sirtalis* and like that described in detail by Davis and interpreted as mating (shown in his Figure 33, erroneously described as a "copulating pair").

The described "copulation" of *Thamnophis radix* fits so exactly the often seen *courtship* of *T. sirtalis*, but is so entirely at variance with the *mating* of *T. sirtalis*, that only one conclusion seems possible: the observer misunderstood the situation, and assumed and recorded copulation when the snakes took the mating position. A brief discussion will make it clear that the account is entirely in accord with our findings for *T. sirtalis* if it is accepted as a description of rather sluggish and unconsummated courtship, rather than of mating.

In the first record of "copulation" of *Thamnophis radix* on April 19, "the day was bright and sunny with a chilly southwest wind and an air temperature between 50° and 60° F." It is known that snakes of the same species in different climates react differently to given weather conditions, but the locality of the observation of *T. radix* is so similar to that where our studies are being made that one would expect similar reactions. Here, copulation on a day of such temperature, especially with a chilly wind, would be unexpected; courtship, however, on such an April day, would be looked for. These facts alone prompted a critical reading of the account, from which it was concluded that in no instance had mating occurred.

On this bright cool day the male found the female and glided along her back. "When the tails of the pair were together, the male stopped and began to bend the rear part of his body around hers. Contact was apparently established almost immediately." But even under perfect weather conditions such quick contact has seldom been seen here; always it has been preceded by at least a brief period of the rhythmic muscular undulations of the male. And almost invariably there is a lash of tails at the moment of attachment which would not have been overlooked. Evidently the contact was assumed by the observer, because of the position of the male's tail.

The account continues with a description of the convulsive waves of the male, "which were interpreted as indicating the actual orgasm." But in *Thamnophis sirtalis* these ripples, varying in frequency and in intensity with varying suitability of weather and season, are the most conspicuous movements of courtship and are practically absent during copulation. When the hemipenis has been inserted the male almost invariably slips off the female at once,

the attachment at the vent being the only point of contact. Evidently these snakes were not in copulation.

If it is realized that in courtship the male's tail keeps moving, bending down about the female's vent now on one side now on the other, the further account is understandable: "After a dozen or more contractions of his body, the male withdrew the hemipenis, turned his body, and seemed to make a new entry with the opposite hemipenis. . . . After about a dozen orgasms in the new position the pair separated voluntarily and the male moved away." That this was a rather half-hearted courtship, such as is not consummated, is shown by the comparative quietness of the male's tail and, further, by the fact that the male wandered away.

When a second male, even more apathetic than the first, made an "attempt to copulate," the first returned quickly and "mated for the second time. Ten minutes later the three snakes were lying quietly near one another [a definite indication that conditions were not right for mating]. At a slight disturbance the first male left. The second male immediately went through the courtship activities, running his chin along the back of the female from a point near the base of her tail until he had reached a position suitable for mating. Copulation took place at once, following the same pattern as that described for the first male. The hemipenes were employed successively as before. The first male returned and tried to effect an entry from the opposite side, but was unsuccessful." From comparisons already made it must be plain that this female was not in copulation five times, as supposed, but was merely the object of languid courtship by two males.

The female of the pair recorded as "in copulo" on May 10 "left quickly when they were disturbed. The pair apparently broke readily, for the male was not dragged by the female, as has frequently been described." The implication is that this pair, too, were in the position of courtship; this, and the fact that the female could leave quickly, suggest that there really was no attachment. If an attached pair is taken in the hands (as can be done in the pits without disturbing them when their heads are hidden in the leaf pile) a fairly strong pull can be given without separating them — a strain which even seems to threaten rupture of the soft tissues of the male. At separation the hemipenis is not seen, which indicates that it is reverted (as would seem from its structure to be the only possible

manner of separation) rather than withdrawn. Thus the female in copulation cannot dart away from the male, unless he simultaneously reverts the hemipenis.

THE FEMALE'S PART

The part played by the female is not clear. Her usual reaction to the arrival of the male is only the watchfulness caused by any other slight disturbance. Rarely, among the hundreds of times that a male has been dropped into a female's pit, has the female made a perceptible advance toward the male before she was found by him. One female arched her tail in an unusual way, took on a most alert manner, and moved slowly in jerks toward the male; another moved slowly to the male and crawled back and forth over him, with the vent slightly open, and copulation occurred within a few seconds. But such behavior is exceedingly rare; as a rule the female lies still until found by the male, unless she has been disturbed by his fall onto the leaves. When he stumbles upon her she may continue to lie still and accept the courtship or she may take flight, sometimes violently lashing her tail or vibrating its tip. This vibration certainly is a recognition of the male, and perhaps a rebuff, for it has been noticeable in females refusing to mate. Subsequent behavior seems to indicate that when a female flees, as is frequent, this is not an invitation for attention, but is an escape. Young females, probably immature, have been seen to do this, and also females already mated; and it is quite common behavior when the season has advanced too far for copulation.

During an accepted courtship the female seems quite passive. But that the male is entirely responsible for that position of the female tail which is necessary for the entrance of the hemipenis, or, in other words, that he can force the mating, seems doubtful, for apparently a female may quietly resist copulation indefinitely. The fact that a capable male may work actively for an hour or more and give up without securing an attachment indicates either that the female has some active part in the final maneuver or, more likely, that she may resist or allow it at will, rather than that she has no voluntary part in it. At times a female which has lain perfectly still during persistent activity of the male for a long time will suddenly dart away, perhaps with a vibrating or lashing of her tail, as though the male had nearly accomplished copulation. And the recorded instances of males found in copulation with dead females seem to

indicate that females have no active part in the maneuver of attachment, but resist or not, at will.

Thus it appears that the female may have an active part in the act of copulation, stimulated to cooperation by the courtship actions of the male, but that more likely she has only the choice of resisting or not a manipulation which throws her into position for entrance of the hemipenis. It would seem to be correct to say that a female accepts copulation, or refuses it.

DURATION OF COPULATION

In only about half the matings has the duration of the attachment been recorded. When several pairs which are being watched are in different pits it is very easy to miss seeing either the starting

TABLE 1

DURATION OF COPULATION OF *THAMNOPHIS SIRTALIS SIRTALIS* AS SHOWN BY 53 MATINGS

Duration of copulation, in minutes	*Number of instances*			
	Total number		*Number followed by birth of young*	
5	1			
6	..			
7	2			
8				
9	2	13		
10	4		3	
11				5
12	2		1	
13	2		1	
14				
15	8		5	
16	7		5	
17	4		1	18
18	4	33	2	
19	1		1	
20	9		4	
21				
22				
23	1			
24	2		1	
25				
26		7		3
27	2		1	
28				
29				
30	2		1	

or the ending of the copulation, and often, too, the snakes are out of sight under the leaves when they separate.

Duration of copulation, as shown by records of 53 matings, is usually from fifteen to twenty minutes (see Table I). About two thirds of the instances (33 of the 53) fall within these limits. Of these 53 matings 26 were followed by fecundity and of these, likewise, about two thirds (18 of the 26) came within the limits of fifteen to twenty minutes.

It may be noted that three successful copulations lasted only ten minutes, but that none of the five which lasted less than ten minutes produced young. The minimum time for successful impregnation may, therefore, be assumed to be about ten minutes. Possibly, however, insemination is immediate and quickly completed, and further attachment serves some other purpose. If this is so, the five-minute copulations may be brief because they are noneffective, rather than noneffective because they are brief.

TABLE II

A Comparison in Respect to Duration of Copulation of All Males of *Thamnophis sirtalis sirtalis* with Two or More Complete Records in the Years 1932–39 Inclusive

Other copulations of these males are not included because the duration was not recorded. Heavy type indicates that a brood was born in the summer following this copulation; light type, that the copulation failed to produce young; and (D), that the female died before time for giving birth, and no record was secured.

Male	*Approximate length of male, in mm.*	*Duration of attachment, in minutes*
Small Brown	500	***7, 10**
TC	574–600	***5, 15, 15 +, 16, 16**
12–12	665 (about)	9 (D), 15 (D), 20
6,13,16–0	690 (?)–709	**15 +, 18** (about)
2,8–10	625–655 (?)	**16, 16**
3,9–0	638	**15, * 17**
L. Black	654–677	15, 17, 20
Brown	565–592	**10, 15, 15, 15, 16,** 17, 18, 30
0–2,6	675	**12,** 21 (D), **24** (about)
D	640–670	9 (an autumn mating), **20, 20, †20 +, 24**
U	735	**20,** 20
2–4,10	Rather small	**20,** 23 (D)
TB	690	20, **30 −, 30 +**

* Second mating of this male on this afternoon.
† Third mating of this male on this afternoon.

There is some indication in Table II that males vary in respect to duration of attachment, but the data are hardly sufficient to warrant more than a comment. The last four males listed in the table certainly seem to have had a tendency to remain attached longer than the average time, especially TB, which was twice recorded as in copulation for about thirty minutes — once being interrupted at the end of that time. It is noticeable that (excepting 2 4,10) these males with long duration are especially large, and that the smallest male, Small Brown, only 500 mm. long, remained attached for a short time, though his ten-minute copulation produced a brood.

USE OF THE TWO HEMIPENES

Only very recently has a record been kept of which hemipenis is used in a mating, and the data are scant. It seems that the two are

TABLE III

A Record of Copulations of Males of *Thamnophis sirtalis sirtalis* Which Mated More than Once in a Season, Showing Which Hemipenis Was Used in Each Instance

Male	Date	Hemipenis used	Duration of attachment in minutes
12–12	March 28, 1938	Right	20
	April 21	Left	15
	April 26	Left	9
W. Black ...	March 24, 1939	?	10–15
	April 4	?	?
	April 4	Right	10
	April 22	Left	21 −
L. Black	April 4, 1939	Right	16 +
	April 13	Right	17
0–2,6	April 20, 1939	Right	21
	April 24	Left	12
	April 25	Right	?
	April 27	Left	24 (about)
2–4,10	April 16, 1940	Left	20
	April 22	Left	23
2–4,6	April 27, 1940	Left	13
	May 9	Left	5 +

used with equal frequency, and that in successive matings they do not regularly alternate — at least if several days have elapsed between. Unfortunately no record of this point was made on the occasions when a male mated twice or three times on the same afternoon. Of the twenty-four records kept during the three years 1938–40, exactly one half show the right hemipenis in use, and one half the left. The individual records of males which mated more than once in a season are given in Table III.

RESULTS OF SUCCESSIVE MATINGS OF A MALE

Certain males, because of their genetical constitutions, were needed for several matings in one season; others were desirable because of their dependability for quickly successful courtship. These considerations, with the need of doing as much as possible in a short time when the day was propitious, led to the use of the same male for a number of copulations in rapid succession. As soon as a good male was free he was put into another pit. In Table IV are recorded the occurrences of two (and, in one instance, three) copulations by the same male, one immediately following the other. Those records in which the second female died before the time for the birth of the young have been discarded from this consideration.

In general the second of the two matings seemed normal in every way, and the broods resulting were of normal size. But two attachments were abnormally brief (five and seven minutes, the usual time being fifteen to twenty), and gave no progeny. Perhaps the previous matings were responsible for the brevity and failure of these two. In the instance in which three copulations were completed within eighty minutes three good broods resulted.

The male's second approach was just as active as the first, and there is nothing to lead one to think that such successive matings are not natural.

THE BIRTH OF THE YOUNG

As reported in an earlier paper (see footnote 2, page 216), the time of birth of young depends on the temperature of the months of May, June, and July, not on the time of mating — provided only that copulation occurs not later than the beginning of the warm weather that starts the preparation of the eggs for ovulation. Matings delayed past this time result in broods born late. The "period

TABLE IV

RECORDS OF TWO (AND, IN ONE INSTANCE, THREE) COPULATIONS BY A MALE OF *THAMNOPHIS SIRTALIS SIRTALIS* IN ONE AFTERNOON

Male	Date	Time	Number of minutes attached	Female	Date of birth of young	Number of young
TB	April 20, 1932	?	20	M	No record	No record
		Immediately after	?	R	Aug. 5	23
D	April 19, 1932	?	20	C	Aug. 31–Oct. 15	13 (all dead)
		?	?	Q	Aug. 4	25
D	April 9 1934	2:16–2:40	24	V	July 24	51
		?	(Brief attachment)	6–2	Aug. 8	13 +
		3:05–3:25	20	W	July 25	35
Brown	April 9, 1934	?	16	B	July 26	24
		?	*	2,6–2	July 24	32
BA	April 26, 1935	1:42–1:57	15	AG	Aug. 12	34
		2:37–2:54	17	2,6–2	Aug. 25	26
Small Brown	May 1, 1936	1:40–1:50	10	7,8–0	Aug. 17	38
		2:08–2:15	7	3,7–0	No brood	0
TC	May 4, 1936	?	?	2,10–2	No record	No record
		40 min. later	5 –†	2,6–2	No brood	0

* Male was twice attached, but dislodged, while TC was attempting attachment.

† Male tried to reattach, unsuccessfully. Very late in the season (May 11), these two snakes mated again and were attached for fifteen minutes or more. This is the only instance, during this work, of a female copulating twice.

of development" (that is, the time between the beginning of preparation of the eggs and the birth of the young, regardless of when fertilization takes place) has varied from three months in a warm season to four months in a cool season.

The number of young has varied from six (the first brood of a female three years old) to fifty-one. Twenty-five to thirty-five is usual. There is considerable difference among broods in the average length of the snakelings. In most broods the males are, on the whole, slightly but significantly larger than the females at birth, but this advantage is lost by the end of the next season, and soon the females are conspicuously larger. A study of the number and size at birth of the snakelings, the sex ratio within the broods, and the rate of growth from birth to maturity and old age has been made, and a report is in preparation.

YOUNG RESULTING FROM MATING IN AUTUMN

On cool sunny autumn days courtship is often seen, and a number of apparently normal copulations have been recorded, in nature and in the snake pits. These are probably effective, for several times a brood has been borne by a female without a spring mating. It could not be said with certainty that such broods resulted from matings of the previous autumn and not from those of the preceding spring. The evidence, however, is strongly against such carrying over of fertility to the second spring, for more than a dozen females known to have mated in the spring and to have had broods in the summer were entirely isolated through the following season and were barren.

There is further evidence against the storing of sperm from spring to spring in the record of a black female with which we worked for several years. One year she had a brood of striped snakelings by a striped male (melanism being a recessive character). The next season, by a black male, all her young were black. The following season she again mated with a striped male, and had only striped young. Apparently the sperm of the preceding season's mating did not function, else her broods would have been mixed in color, "contaminated." This indicates that though sperm may last from an autumn mating to a spring fertilization they apparently do not survive in the female from one spring to the next.

Effective autumn mating is certainly not uncommon, but whether or not it is frequent has not been determined. At different times at

least half a dozen females collected in the fall have had young next season without spring mating. The odd ratios of striped and black young reported by E. B. S. Logier [3] in broods from collected wild black females are difficult to explain unless the broods represented two males. Melanism has been shown to be a simple Mendelian recessive,[4] so if broods from black females have both color patterns, striped and black snakelings should appear in equal numbers. They are anything but this in wild collected females. There seems to be a tendency for recently mated females to avoid another copulation immediately, and we have therefore suggested that the odd ratios, inexplicable on Mendelian lines alone, result from an autumn mating followed by another in the spring, rather than from two spring matings. That sperm should be able to survive the winter is not hard to believe in view of the fact that in very early spring effective mating may occur on a warm day which is followed by cold weather, when the snakes retreat again to hibernation. Broods from such abnormally early activity are not born earlier than those of matings of a month later, which suggests that the sperm hibernate with the female. The question of autumn mating and survival of sperm has been discussed in an earlier paper.[4]

FAILURE OF FEMALES TO HAVE YOUNG

Of fifty-four observed matings in the years 1932–37 inclusive forty gave young and fourteen (or about one fourth) were unproductive. Unusually early matings, after which the females return to hibernation, are not less likely to be productive, for of the four recorded for March 16 and 22 three gave young, which is up to the general average. Of the three very late matings, one produced a normal brood, one female had no young, and one died with no record obtained.

The fourteen failures, which were scattered through the years, may be classed as follows:

1. Three failures which may be attributed to interrupted copulations. In one instance the snakes were frightened by observers

[3] "Melanism in the Garter Snake, *Thamnophis sirtalis sirtalis*, in Ontario," *Copeia*, 172 : 83–84. 1929; "Some Additional Notes on Melanism in *Thamnophis sirtalis sirtalis* in Ontario," *Copeia*, 1 : 20. 1930.

[4] Blanchard, Frank N. and Frieda Cobb, "The Inheritance of Melanism in the Garter Snake *Thamnophis sirtalis sirtalis* (Linnaeus), and Some Evidence of Effective Autumn Mating," *Pap. Mich. Acad. Sci., Arts, and Letters*, 26 (1940) : 177–193. 1941.

(a class) and separated after five minutes. Another pair separated after fifteen minutes, which is a normal time, but the male repeatedly tried to reattach, which is not normal behavior. A third pair separated after seven minutes, for no evident reason. This was the second mating of the male, and followed immediately on the first, which lasted ten minutes and was successful. Since in other instances an immediate second mating by a male has profound results the seven-minute copulation was probably not complete.

2. Three failures which may perhaps be attributed to old age of the female. One of these females had been kept in our pits for fifteen years and could not well have been less than five years old when caught, making an age of at least twenty years. She had borne young regularly for the six years previous to this failure, but the following autumn she was in poor condition and instead of hibernating normally she stayed out, and died. The age of a second old female we do not know, but her very great size (1,104 mm.) suggests great age. She was caught on May 14 after the mating season, yet bore no young that year. The following season she copulated with a male of good record, but had no young. Perhaps she had reached sterility. The third of these females was also exceedingly large (974 mm. the previous autumn). She did bear a brood of thirty-three the year following this failure, as was true, but though we were able to keep her for three years after that, we were not able to accomplish even a mating.

3. Three failures in which the mating records were not normal. One pair was in copulation for fifteen minutes, but the male had worked hard for an hour previously. Though the conditions were favorable, without response from the female. Another of these three was the only instance we have observed of a female mating twice. The two snakes were in copulation for five minutes on May 4 (forty minutes after the start of a previous copulation by the male). The male tried to reattach, and we assumed this to indicate incomplete insemination. On May 11 (a very late date for mating) we introduced the male again and a fifteen-minute copulation resulted. Even so, there was no brood. A third female had had a brood without a spring mating. The following spring an apparently normal mating occurred, but there were no young. The next spring, however, she refused to mate and in the autumn had to be killed because of an unhealthy skin condition.

4. Three failures which could not be accounted for, but in which there was no brood history for the females. One rather large female (mating with a very small male, possibly not mature and with no other mating record) was kept for four years, during which this was her only copulation, so there is no record of her fertility. Another of these females had been born in 1923 and was at this time nine years old and 615 mm. long, but had never before mated. The next year she mated again, but died soon afterwards, never having produced young. Here again there is no record of fertility. The last of these three females had been caught the year before, and this was the only season that she mated in the pits.

5. Two failures for which there is no evident excuse. The duration of copulation was recorded as normal in one instance (and not recorded as abnormal in the other), and the dates were normal; the male had a good fertility record, and had not just previously mated; each female had a good record, had borne young the year preceding, and bore the year following. But here it is interesting to note that in two other instances a pair of snakes which had been confined together constantly, failed to produce young one year though they had the year preceding. It is not known whether unfruitful copulations occurred or whether the snakes did not mate. But these two failures, in addition to the two unaccountable failures under discussion, suggest that it may not be abnormal for a female to omit a year occasionally.

It has been noticed at the Biological Station of the University of Michigan that many of the garter snakes caught in the pits well after the mating season is over and too early for the young to have been born from spring matings have no developed embryos or bear no young. Of course it is not known whether or not these snakes mated.

* * * * *

1. Under the fairly natural conditions of the enclosures at Ann Arbor, Michigan, mating occurs on days of suitable weather from mid-March to early May, especially in late April. After this period females which have not mated will not do so, and males soon cease courtship.

2. In the autumn the garter snakes have another mating period. Snakes caught in the late autumn, though prevented from mating the

next spring, may have young in the summer. But captive females, without autumn mating, have not borne young from the spring mating of the previous year. This indicates that autumn mating may produce young, sperm presumably hibernating in the female.

3. Courtship, more or less vigorous, often occurs when conditions are not suitable for copulation; it may last for hours, wane, and end unconsummated. When conditions are right it may be as brief as two or three minutes, though that is not usual. During a courtship which ends with copulation the female is usually quiet or moves slowly, while the male is very active, maintaining or repeatedly resuming his superior position, often quickly "chinning" his way toward her tail, suddenly reversing, and coming back to the original position with convulsive body ripples running forward from his tail.

4. After attachment has been secured, the male slides from the back of the female and is generally quite passive, his rhythmic convulsive waves ceasing. These waves are apparently connected with courtship, not with insemination.

5. Attachment commonly lasts from fifteen to twenty minutes, but has varied from five to thirty. Those lasting less than ten minutes have not produced young.

6. Only one hemipenis is used in a mating. The two are used with about equal frequency, but probably not alternately.

7. The female's part in copulation appears to be passive; she accepts or resists it, but probably has no active part in it.

8. After separation the male may immediately mate with another female, and even a third, producing young; but the female does not mate again — or at least not immediately.

9. The broods of females which mate in late April are born from three to four months later, the date of birth depending on the summer temperature. The number of young in a brood has varied from six (the first brood of a three-year-old female) to fifty-one. The broods differ considerably in the average length of the snakelings. Males are slightly longer at birth.

10. About one fourth of the recorded matings gave no young. Some failures may be attributed to interrupted copulation, old age of the female, or some abnormal condition or circumstance; but for others there is no evident excuse. In nature it has been observed that many adult females are barren.

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THE PALPIMANIDAE OF PANAMA

ARTHUR M. CHICKERING

PETRUNKEVITCH (1911) listed only four genera and seven species of Palpimanidae in his *Index-Catalogue*. Five of these species were from South America; two from the West Indies. Three genera were represented by only the type species. Banks (1929) found one female on Barro Colorado Island, Canal Zone, in June, 1924, and described it as a new species, *Otiothops macleayi*. Dr. Frank E. Lutz, of the American Museum of Natural History, found a single female in June, 1915, on the island of Porto Rico, and Petrunkevitch (1929) described it as *O. lutzi*. Bryant (1940) recorded three females of *O. walckenaeri* MacLeay and also the allotype male in her extensive collections from Cuba.

Otiothops macleayi Banks appears to be the only palpimanid occurring in the regions of Panama where I have collected. The species is common on Barro Colorado Island along the fringe of the cleared land in the vicinity of the laboratory buildings of the Canal Zone Biological Area, and I now have many specimens of both sexes from several localities in Panama, as recorded later in this paper.

The most important features of the family may be summarized as follows: only two spinnerets; the eight eyes heterogeneous and in two rows; either two or three tarsal claws; no epigynum; male palp simplified; maxillary lobes convergent; anterior tarsi and metatarsi provided with heavy prolateral scopulae; three pairs of cardiac ostia.

A male has been selected as the allotype and described as follows:

Otiothops macleayi Banks

(Figures 1–5)

Male allotype. — Total length 6.7 mm. Carapace 2.695 mm. long, 1.96 mm. wide opposite second coxae, almost perfectly oval as seen from dorsal view; posterior eyes occupying slightly less than nine elevenths of width of head; thoracic groove represented by a fairly

deep fovea at bottom of first abrupt declivity; very gently arched from posterior row of eyes to beginning of last fourth, then abruptly declivitous to fovea, and, after that, more gently sloping to posterior border (Fig. 4); about two thirds as high as wide.

Eyes. — Eight in two rows. Posterior row only slightly longer than anterior row. Observed from above, anterior row somewhat recurved; posterior row strongly procurved, so that lateral eyes

EXTERNAL ANATOMY OF *OTIOTHOPS MACLEAYI* BANKS

(Figures 1–5)

1. Male palpus, retrolateral view
2. Male palpus, ventral view
3. First femur, retrolateral view
4. Cephalothorax, lateral view
5. Fang groove with retrolateral teeth and cluster of spines

are practically contiguous. AME round, LE oval, PME irregularly oval. PME silvery, all others transparent. Ratio of eyes AME : ALE : PME : PLE = 7 : 5 : 5 : 4.5. AME separated from one another by six sevenths of their diameter, from ALE by five sevenths of their diameter. PME separated from one another by two thirds of their diameter, from PLE by twenty ninths of their diameter. Laterals separated only by a line. Central ocular quadrangle wider in front than behind in ratio of 4 : 3; almost exactly

as long as wide in front. Width of clypeus equal to eighteen sevenths of diameter of AME. Ventral third of clypeus excavated and fringed with a thin whitish membrane (clypeal excavation much less evident in female holotype).

Chelicerae. — Short, stout, with short fang; distinct ridgelike boss; roughened and irregularly corrugated on anterior surface. Promargin of fang groove without teeth; retromargin with four small teeth (Fig. 5). Peculiar cluster of nine stiff spines opposite tip of fang (teeth and spines determined from a paratype to avoid injury to the allotype, but confirmed on the latter). Females frequently with five teeth on retromargin as well as cluster of spines.

Maxillae. — Longer than wide in ratio of slightly more than 2 : 1; rounded along outer border, which is strongly chitinous distally. Well-developed scopulae along mildly truncated distal medial corners. A low tooth where maxillae meet a corresponding rough tubercle on sternum. Moderately convergent.

Lip. — Generally triangular in shape, longer than wide in ratio of 19 : 17; distal end deeply notched. About four fifths of length of maxilla. Distal half gently excavated laterally and gently keeled centrally. Sternal suture slightly procurved. Rostrum projects beyond tip of lip.

Sternum. — Longer than wide in ratio of 30 : 21, widest between intervals separating first and second legs. Convex, beaded, strongly chitinized parts extending dorsally between legs to membrane separating sternum from carapace, continued between fourth coxae, where it is truncate; fourth coxae separated by almost their greatest diameter. Two small teeth near posterior truncature. First coxae nearly twice as long as either second or third, and much stouter.

Legs. — 4123. Tibial index of first leg 14, of fourth leg 11.

	Femora	*Patellae*	*Tibiae*	*Metatarsi*	*Tarsi*	*Totals*
	(All measurements in millimeters)					
1.	1.84	1.60	1.22	0.55	0.66	5.87
2.	1.43	0.88	1.16	0.95	0.55	4.97
3.	1.59	0.70	0.98	0.87	0.50	4.64
4.	1.67	0.98	1.51	1.47	0.61	6.24
Palp	0.65	0.18	0.28	...	0.70	1.81

Width of first patella at knee 0.405 mm.; width of fourth patella at knee 0.27 mm. First femora very stout, very convex dorsally on proximal halves (Fig. 3); greatest dorsoventral diameter 0.96 mm.,

or slightly more than one half total length of segment. Relative lengths of leg segments, as shown by table above, often very different from what is usual in spiders. No spines. First leg with true scopulae as follows: complete iridescent prolateral tibial scopula; complete iridescent prolateral metatarsal scopula; small iridescent prolateral tarsal scopula on second quarter; small distal tarsal scopula of very short tenent hairs. Second leg with a ventral metatarsal brush of hairs along distal half of segment, also with a short distal tarsal scopula. Third and fourth legs same as second. Elsewhere legs covered with a moderately heavy coating of fairly long hair. Trichobothria apparently lacking. Two curved claws throughout, seemingly alike; terminal tooth stout, longest; eight or nine others shorter, smaller, becoming retrocurved toward base. Claw tufts small on posterior two pairs of legs; normal on anterior two pairs.

Palp. — Small, simple, with no apophyses. Femur somewhat curved dorsally. Cymbium long and slender, somewhat constricted at about two fifths of distance from base; with a retrolateral band of stiff black bristles. Bulb ovoid, with embolus originating from outer side near basal end and extending in slightly sinuous fashion to near tip of cymbium, where it divides into two very slender processes, one straight, pointed, the other curved (Figs. 1–2).

Abdomen. — Regularly ovoid, only slightly flattened ventrally; quite thickly clothed with hair. Epigenital area strongly chitinized and irregularly corrugated. Chitinized epigenital area extends dorsally into a short but well-marked scutum. No colulus visible. Single pair of spinnerets short, tubular. Anal tubercle short, blunt.

Color in alcohol. — Both carapace and sternum a rich reddish mahogany color, as are the first pair of legs, chelicerae, epigenital area, abdominal scutum, maxillae, and lip. Remaining legs and palps a light amber. Abdomen, except as otherwise noted, a duller reddish brown with yellowish dots.

Type locality. — Male allotype from Barro Colorado Island, Canal Zone, August, 1939. I now have in my collection ninety-four mature specimens of both sexes from the following localities: Barro Colorado Island, 1934, 1936, 1939; Porto Bello, 1936; Canal Zone Forest Reserve, 1939; Madden Dam region, 1936, 1939; Balboa, 1939.

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AGE AND GROWTH OF THE YELLOW PERCH, *PERCA FLAVESCENS* (MITCHILL), IN THE WISCONSIN WATERS OF GREEN BAY AND NORTHERN LAKE MICHIGAN

RALPH HILE AND FRANK W. JOBES

INTRODUCTION

ALTHOUGH the yellow perch occurs in the shallower waters throughout the Great Lakes and is of considerable importance to both commercial fishermen and anglers in many localities, the chief centers of commercial production are Lake Erie, Saginaw Bay in Lake Huron, and Green Bay in Lake Michigan. Investigations of the age and growth of yellow perch in Great Lakes waters have been made of the Lake Erie perch by Jobes (MS) and of the Saginaw Bay perch by Hile and Jobes (1941).[1] The completion of the present study, the first on the growth of yellow perch in Lake Michigan, makes possible a comparison of the growth of the species in the three leading centers of production in the Great Lakes.

The study of the growth of the Green Bay yellow perch is of particular significance because of the contention of Wisconsin fishermen that this stock of perch grows at an exceptionally slow rate. The Green Bay fishermen believe also that the perch grows more slowly in the bay than in the open waters of Lake Michigan.

MATERIALS AND METHODS

The determination of age and the calculation of individual growth histories from the examination and measurement of scales were carried out for 752 yellow perch collected in Green Bay (see Fig. 1 for localities). An additional 90 fish, for which there were no sex

[1] Hile, Ralph, and Jobes, Frank W., "Age, Growth, and Production of the Yellow Perch, *Perca flavescens* (Mitchill), of Saginaw Bay," *Trans. Am. Fish. Soc.*, 70: 102–122, figs. 1–5. 1941.

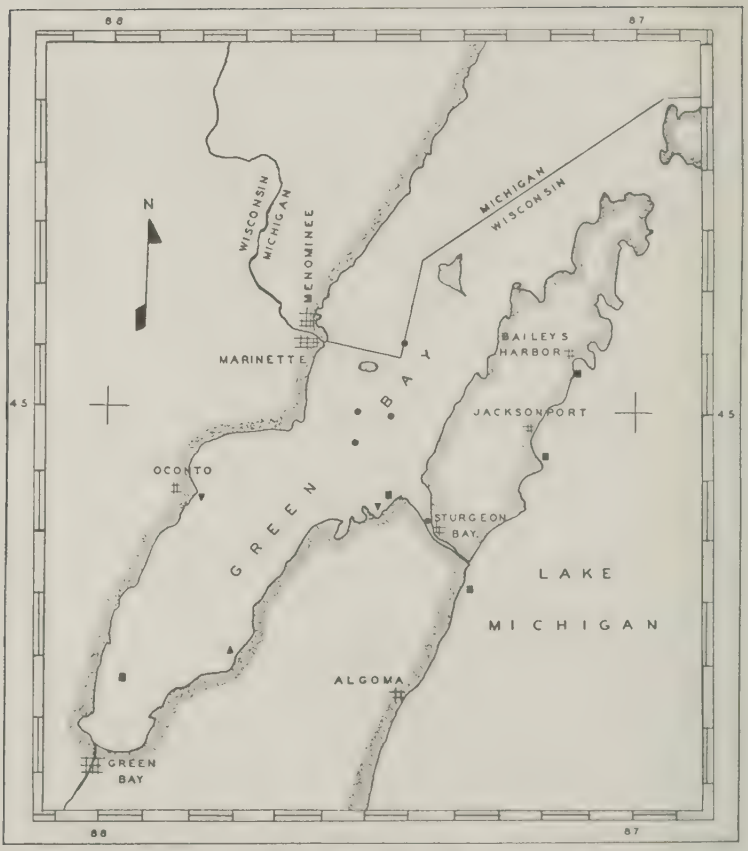

FIG. 1. Localities at which samples of eighteen or more yellow perch were taken in Green Bay and Lake Michigan: 1932, circles; 1934, upright triangles; 1937, squares; 1938, inverted triangles

data, were employed in the study of age composition (Table I), but their individual growth histories were not computed. All but the 1932 collections were taken in commercial gear. The details concerning the collections follow:

1932: 441 perch taken between April 27 and May 23, in experimental gill nets (mesh sizes: $2\frac{3}{8}$, $2\frac{1}{2}$, $2\frac{5}{8}$, and $2\frac{3}{4}$ inches, extension measure) fished from the Bureau of Fisheries vessel, *Fulmar.*

1934: 107 perch taken on March 24 in a 2–2¼-inch-mesh pound net.
1937: 55 perch taken between November 26 and December 3 in a 2⅜-inch-mesh gill net and 3 (not included in Tables I and II, but included in body of Table IV) in a 2⅝-inch-mesh gill net; 74 fish taken on December 13 by a 2¼-inch-mesh fyke net (includes one fish without sex data, not used in the growth study). Eighty-nine fish for which sex data were lacking, taken on November 12 in a 2⅜-inch-mesh gill net, were employed for the study of age composition but not of growth.
1938: 73 perch taken between March 22 and April 5 in pound nets and fyke nets whose mesh sizes ranged from 1¾ to 2⅝ inches (more than half of the total from a 2-inch-mesh pound net).

In addition, ages were determined for five large fish selected for size.

The study of the relationship between the length and the weight of Green Bay yellow perch was based on 938 fish, including all specimens employed in the investigation of age and growth and also those perch whose ages could not be determined and several scattered selected samples (large fish selected for size, samples of illegal fish only, samples of legal fish only).

The relationship between total length and standard length was determined from measurements of 509 yellow perch from Green Bay and 360 from the Beaver Island region of northeastern Lake Michigan. No significant differences were found between the data from the two areas.

Collections of yellow perch totaling 276, taken in 2⅝-inch-mesh commercial gill nets between September 2 and October 13, 1937, were employed for the study of the age and growth of the perch in the Wisconsin waters of northern Lake Michigan (see Fig. 1 for localities). Ages of four large selected fish collected in 1937 and 1938 were also determined. The investigation of the length–weight relationship of perch in this area was based on 294 fish.

Scales for age determination were mounted in a glycerin-gelatine medium and examined and measured on a microprojection apparatus at the magnification × 40.7. The calculation of growth was made by the method employed for the Saginaw Bay yellow perch (see note 1). In this procedure direct-proportion computations, based on the assumption that the body-scale ratio is constant, were employed for the determination of calculated lengths of 102 millimeters and greater. Calculated lengths less than 102 millimeters were "corrected" to compensate for the disproportionate growth of body and scale among smaller fish. It is realized that the correction of

the calculated lengths of the Green Bay and Lake Michigan yellow perch from a body scale curve derived from Saginaw Bay materials may involve a certain degree of approximation. It is not believed, however, that the error was large.

Ages have been designated by roman numerals corresponding to the number of annuli on the scales, except for fish taken in the spring before the onset of growth. For these fish an annulus was "assumed" to be present at the edge of the scale, and the age assigned exceeded by one the number of visible annuli.

All materials and data obtained from Lake Michigan in 1937 and 1938 and from Green Bay in 1934, 1937, and 1938 were collected by investigators of the Wisconsin Conservation Department and made available to us through the courtesy of Dr. Edward Schneberger, chief of the Biology Division. The 1932 collections were made by Dr. Hilary J. Deason and other staff members aboard the Bureau of Fisheries vessel *Fulmar*. We wish also to thank Dr. John Van Oosten, in charge of Great Lakes Fishery Investigations of the U. S. Fish and Wildlife Service, for his numerous suggestions for the improvement of the original manuscript.

AGE COMPOSITION AND LENGTH DISTRIBUTION

The age composition of the samples of Green Bay yellow perch (Table I) varied widely, with the dominant age group as young as II and as old as V. The 1932 data suggest that mesh size of the gill nets employed had a significant effect on the age composition of the samples. The samples from the $2\frac{3}{8}$-inch-mesh net were dominated by age group IV, whereas the samples from the larger mesh sizes all were dominated by age group V. The relative abundance of IV-group perch tended to decrease and the abundance of VI-group fish to increase with increase in the size of mesh.

Dominant age groups in samples from commercial gears (the $2\frac{3}{8}$-inch-mesh experimental gill net fished in 1932 may be considered commercial gear) were age group II in the gill-net sample of 1937, age group III in the fyke-net collection of the same year and the pound-net collection of 1934, and age group IV in the collections of 1932 and 1938. It should be mentioned, however, that the 1937 collections were made in late fall and early winter, whereas the collections of the remaining years were taken in the spring. Consequently fish captured in 1937 had enjoyed one more season of growth

TABLE I

Age Composition of Samples of Green Bay Yellow Perch Taken in Different Calendar Years, in Different Seasons, and by Different Fishing Gear (Percentages in Parentheses)

Year and season	Kind of net, and mesh size in inches	Age group									Total
		I	II	III	IV	V	VI	VII	VIII	IX	
1932 (spring)	$2\frac{3}{8}$ gill	...	2 (1.6)	2 (1.6)	68 (53.1)	41 (32.0)	14 (10.9)	1 (0.8)	...	...	128
	$2\frac{1}{2}$ gill	...	...	2 (1.9)	32 (31.1)	43 (41.8)	26 (25.2)	...	...	...	103
	$2\frac{5}{8}$ gill	...	...	1 (1.0)	27 (27.3)	50 (50.5)	21 (21.2)	...	...	...	99
	$2\frac{3}{4}$ gill	...	1 (0.9)	1 (0.9)	21 (18.9)	53 (47.8)	31 (27.9)	4 (3.6)	...	...	111
1934 (spring)	2–$2\frac{1}{4}$ pound	...	26 (24.3)	41 (38.3)	35 (32.7)	4 (3.8)	...	1 (0.9)	...	...	107
1937 (fall)	$2\frac{3}{8}$ gill	...	71 (49.3)	55 (38.2)	14 (9.7)	4 (2.8)	...	...	...	...	144
	$2\frac{1}{4}$ fyke	2 (2.7)	21 (28.4)	44 (59.5)	7 (9.4)	...	...	...	...	...	74
1938 (spring)	$1\frac{3}{4}$–$2\frac{5}{8}$ impounding	...	...	1 (1.4)	41 (56.2)	18 (24.6)	6 (8.2)	2 (2.7)	4 (5.5)	1 (1.4)	73
1932–38 (spring–fall)	All commercial gear *	2 (0.4)	120 (22.8)	143 (27.1)	165 (31.4)	67 (12.7)	20 (3.8)	4 (0.8)	4 (0.8)	1 (0.2)	526

* Excludes catches of $2\frac{1}{2}$-, $2\frac{5}{8}$-, and $2\frac{3}{4}$-inch-mesh gill nets in 1932

than had members of the same age groups in the collections of other years. A better idea of the age composition of the commercial catch may possibly be obtained from a compilation made in terms of completed growing seasons (Table II).

Yellow perch that had completed four seasons of growth made up nearly half (46.2 per cent) of the combined samples of the commercial catch. Next in abundance were perch that had completed three growing seasons (25.8 per cent) and five growing seasons (16.0 per cent). Other groups were represented only sparsely.

TABLE II

Age of Green Bay Yellow Perch Taken in Commercial Gear, Expressed in Terms of the Number of Growing Seasons Completed

Number of completed growing seasons	*Number of fish*	*Percentage*
2	30	5.7
3	136	25.8
4	243	46.2
5	84	16.0
6	24	4.5
7	4	0.8
8	4	0.8
9	1	0.2

The age composition of the samples collected with 2½-inch-mesh gill nets in Lake Michigan in the fall of 1937 may be seen in Table III. Age group IV was dominant (42.7 per cent), and the combined age groups III and IV made up 78.2 per cent of the total. The only samples from Green Bay from 2½-inch-mesh gill nets (spring of 1932) were dominated by age group V. In terms of seasons of growth completed, however, these V-group fish correspond to the IV-group perch captured in Lake Michigan in the fall.

It is not believed that the data on the age composition of the samples of yellow perch from either Green Bay or Lake Michigan are suitable for an analysis of the relative abundance of the year classes represented. The chief defect of the data is the lack of adequate collections taken over a period of consecutive years by means of gear of the same type and mesh size. A further weakness of the data for the Green Bay perch lies in the fact that most of the collections were taken during the spawning run. In spawning-run samples the younger age groups that contain a high percentage of immature fish are not adequately represented.

TABLE III

AGE COMPOSITION OF THE SAMPLES OF YELLOW PERCH TAKEN IN THE FALL OF 1937 IN THE LAKE MICHIGAN WATERS OF DOOR COUNTY, WISCONSIN

Age group	*Number of fish*	*Percentage*
II	25	9.1
III	98	35.5
IV	118	42.7
V	27	9.8
VI	8	2.9

The length–frequency distributions of Green Bay yellow perch have been arranged in Table IV according to sex and the number of completed growing seasons (that is, with perch collected in the fall of 1937 combined with fish of the next higher age group of the spring collections of other years). As is commonly true of perch, the length distributions of fish of different ages exhibited considerable overlap, although this overlap doubtless was increased in the data for Green Bay perch by the combination of samples taken in different calendar years. All length intervals at which fish were abundant were represented by perch of three or four different ages. In fish of corresponding age the modal and average lengths of females consistently exceeded those of males.

Females attained the State of Wisconsin's legal size of $7\frac{1}{2}$ inches, total length (162 millimeters, standard length), earlier than males. (Although a 7-inch limit was in effect at the time of the collection of the materials employed in this study, the limit was raised to $7\frac{1}{2}$ inches on July 1, 1940, and is scheduled to be increased further to 8 inches, effective on July 1, 1943.) At the end of two growing seasons all males and females were below legal length. On the completion of three growing seasons, however, 96.0 per cent of the males though only 53.8 per cent of the females were undersized. Relatively few of the females (9.0 per cent) but a majority of the males (57.6 per cent) were below the length of $7\frac{1}{2}$ inches at the end of four growing seasons. Undersized perch of both sexes were scarce at the end of five and six growing seasons (no undersized females at the end of six seasons), and all fish were longer than $7\frac{1}{2}$ inches beyond the sixth year of life.

In the third and fourth columns from the right of Table IV may be seen the length–frequency distribution of all random samples of

TABLE IV

LENGTH FREQUENCY DISTRIBUTION OF GREEN BAY YELLOW PERCH (COLLECTIONS OF ALL THE YEARS COMBINED) ACCORDING TO SEX AND THE NUMBER OF COMPLETED GROWING SEASONS

At right, the length distribution of all samples from commercial gear in Green Bay and the length distribution of all samples from commercial gill nets in Lake Michigan

Standard length in millimeters	Age in completed growing seasons														Length distribution of commercial catch			
	2		3		4		5		6		7		8	9	Green Bay		Lake Michigan	
	M*	F*	M	F	M	F	M	F	M	F	M	F	F	F	Number†	Percentage	Number‡	Percentage
100–109	5	4	..	..	..	..	..	..	..	..	..	..	..	..	8	1.5	..	..
110–119	6	11	1	..	..	..	..	..	..	..	..	..	..	..	16	3.0	..	...
120–129	1	2	6	2	..	..	..	..	..	..	..	..	..	..	10	1.8	..	...
130–139	..	..	7	8	5	..	..	..	..	..	..	..	..	..	19	3.5	..	...
140–149	..	..	8	7	8	3	..	..	..	..	..	..	..	..	36	6.6	..	...
150–159	..	1	2	8	18	13	1	1	..	..	..	..	..	..	79	14.6	3	1.0
160–169	..	1	1	12	10	34	8	3	1						98	18.1	13	4.5
170–179	..	..	..	6	9	44	4	10	1	1	..	..	..	..	83	15.3	71	24.5
180–189	..	..	..	5	4	50	4	18	4	6	..	..	..	..	82	15.1	84	29.0
190–199				2	3	37	7	43	5	7	1	1			51	9.4	50	17.3
200–209	..	..	..	2	1	33	10	42	5	18	.				27	5.0	44	15.2
210–219	..	..	..	..	1	22	7	40	2	20	..	..	..	..	7	1.3	10	3.5
220–229	..	..	..	..	..	6	1	16	4	14	1	..	..	..	6	1.1	9	3.1
230–239	..	..	..	..	..	1	..	4	1	7	1	..	..	..	3	0.5	..	...
240–249	..	..	..	..	..	1	..	4	1	3	..	..	1	..	5	0.9	1	0.3
250–259	..	..	..	..	..	..	..	1	..	..	..	1	..	..	2	0.4	3	1.0
260–269	..	..	..	..	..	..	..	1	..	1	..	2	..	..	4	0.7		.
270–279	..	..	..	..	..	..	..	1	..	..	..	1	..	..	1	0.2	..	...
280–289	..	..	..	..	..	..	..	..	..	..	..	..	2	..	2	0.4	1	0.3
290–299	..	..	..	..	..	..	..	..	..	1	..	..	..	1	2	0.4	1	0.3
300–309	..	..	..	..	..	..	..	..	..	..	..	..	1	..	1	0.2	..	...
Number of fish	12	19	25	52	59	244	42	184	24	78	3	5	4	1	542	100.0	290	100.0
Average length	111	118	137	161	162	186	190	204	204	213	216	258	279	294	172		190	
Percentage illegal §	100.0	100.0	96.0	53.8	57.6	9.0	7.1	1.1	4.2	0.0	0.0	0.0	0.0	0.0	30.8		1.4	

* M = male; F = female † Includes 16 fish whose ages were not determined
‡ Includes 14 fish whose ages were not determined § Less than 7½ inches, total length (162 millimeters, standard length)

Green Bay yellow perch taken in commercial gear. The percentage of undersized fish ($7\frac{1}{2}$-inch size limit) in the samples of the commercial catch was 30.8. The percentages of illegal-sized perch at size limits of 7, 8, and $8\frac{1}{2}$ inches (an $8\frac{1}{2}$-inch size limit is effective in the State of Michigan waters of the Great Lakes) were 21.5, 49.2, and 67.3, respectively.

The additional information that would be obtained from the presentation of length frequency distributions of the age groups of Lake Michigan yellow perch is not sufficiently great to warrant the expansion of the tabular material. The length frequency distribution of all Lake Michigan perch, however, is shown at the extreme right of Table IV. Of the 290 perch (including 14 whose ages were not determined) in samples of the commercial catch (taken by $2\frac{3}{8}$-inch-mesh gill nets) only 1.4 per cent were below $7\frac{1}{2}$ inches in length. At size limits of 7, 8, and $8\frac{1}{2}$ inches the percentages of illegal-sized fish were 0.0, 9.0, and 34.8, respectively.

GROWTH IN LENGTH AND WEIGHT

The average lengths and weights of the age groups of Green Bay yellow perch at capture and the calculated growth histories of the age groups are given for the males in Table V and for the females in Table VI. The calculated lengths in these two tables exhibit numerous and at times large discrepancies. Some of these disagreements are doubtless the result of the small numbers of specimens in certain age groups. The remainder must be ascribed to other causes. The discrepancies are in general similar in the data for both sexes.

Lee's phenomenon of "apparent decrease in growth rate" with increase in the age of fish on which the calculations of growth are based occurred in the calculated lengths for the first three or four years of life. The second-year and third-year calculated lengths exhibited these systematic discrepancies most sharply. First-year lengths were affected less and fourth-year lengths only slightly. The calculated lengths in the later years of life gave no indication of the presence of Lee's phenomenon.

A detailed discussion of the probable causes of Lee's phenomenon in the calculated lengths of yellow perch need not be given since the problem has been treated thoroughly by Jobes (MS). Although no study was made of the body-scale relationship in the Green Bay

TABLE V

Average Length and Weight at Capture of Male Yellow Perch from Green Bay and the Average Calculated Length Attained by the Age Groups at the End of Each Year of Life

Age group	Year of capture	Number of fish	Weight in ounces	Total length in inches	Weight in grams	Standard length in millimeters	Calculated standard length in millimeters at end of year of life						
							1	2	3	4	5	6	7
VII	1932	3	6.2	10.0	176	216	57	91	130	151	175	200	216
VI	1932	20	5.9	9.6	167	209	57	93	121	151	180	209	...
	1938	2	3.5	8.0	99	174	62	93	125	144	162	174	...
V	1932	26	5.4	9.4	152	203	59	95	130	165	203	...	...
	1934	2	3.5	8.2	98	178	57	95	130	164	178	...	...
	1937	2	3.9	8.4	110	182	58	89	108	134	160	182*	...
	1938	7	3.4	7.9	97	172	65	99	124	147	172	...	...
IV	1932	7	4.3	8.7	121	189	58	96	140	189	...	...	...
	1934	15	2.1	6.9	59	147	59	94	123	147	...	...	...
	1937	7	3.3	7.7	94	166	62	95	122	148	166*	...	...
	1938	11	2.9	7.6	81	165	64	104	138	165	...	...	...
III	1934	21	1.5	6.3	43	134	66	104	134	...	...	...	...
	1937	26	3.0	7.5	84	163	63	102	136	163*	...	...	...
II	1934	12	0.8	5.2	22	111	67	111	...	...	...	...	...
	1937	4	2.6	7.1	74	154	67	111	154*	...	...	...	...
Grand average calculated length †							62	99	130	159	185	211	227
Annual increment of length							62	37	31	29	26	26	16
Number of fish							165	165	153	128	69	32	3

* Actual length at capture in November and December

† Beyond the fifth year of life the grand average calculated lengths were determined by the successive addition of the grand average annual increments of length to the grand average calculated length at the end of the fifth year

TABLE VI

AVERAGE LENGTH AND WEIGHT AT CAPTURE OF FEMALE YELLOW PERCH FROM GREEN BAY AND THE AVERAGE CALCULATED LENGTH ATTAINED BY THE AGE GROUPS AT THE END OF EACH YEAR OF LIFE

Age group	Year of capture	Number of fish	Weight in ounces	Total length in inches	Weight in grams	Standard length in millimeters	Calculated standard length in millimeters at end of year of life								
							1	2	3	4	5	6	7	8	9
IX	1938	1	24.0	13.5	680	294	55	79	121	165	189	212	236	260	294
VIII	1938	4	18.8	12.8	533	279	60	90	120	172	216	243	264	279	...
VII	1932	2	11.7	11.7	333	254	55	85	126	164	192	225	254	...	...
	1934	1	11.3	12.1	320	264	53	86	132	162	191	244	264	...	...
	1938	2	14.2	11.9	402	259	56	88	118	154	200	236	259	...	...
VI	1932	72	6.3	9.7	179	211	58	92	119	148	180	211	...	...	...
	1938	4	14.0	11.8	398	257	58	90	130	182	225	257	...	...	...
V	1932	161	5.6	9.4	159	204	59	94	129	166	204	...	...	...	...
	1934	2	3.2	8.1	92	175	59	93	116	154	175	...	...	...	...
	1937	1	3.6	8.0	102	173	50	78	112	134	154	173*	...	...	...
	1938	11	9.5	10.3	268	224	64	103	151	194	224	...	...	...	...
IV	1932	141	4.9	9.0	138	195	60	100	144	195	...	...	...	...	...
	1934	20	2.7	7.5	76	162	62	99	134	162	...	...	...	...	...
	1937	10	4.1	8.3	116	180	62	100	129	156	180*	...	...	...	...
	1938	30	3.5	7.9	100	172	64	104	144	172	...	...	...	...	...
III	1932	6	2.9	7.3	81	158	62	108	157	...	...	...	...	...	...
	1934	20	2.1	6.9	59	148	69	107	148	...	...	...	...	...	...
	1937	54	4.0	8.2	112	178	61	101	142	178*	...	...	...	...	...
	1938	1	2.9	7.6	82	165	76	115	165	...	...	...	...	...	...
II	1932	3	0.8	5.2	22	112	68	112	...	...	...	...	...	...	...
	1934	14	0.8	5.3	23	114	67	114	...	...	...	...	...	...	...
	1937	25	3.4	7.9	95	171	68	116	171*	...	...	...	...	...	...
I†	1937	2	2.5	7.2	71	156	72	156*	...	...	...	...	...	...	...
Grand average calculated length ‡							61	99	137	173	197	228	251	268	302
Annual increment of length							61	38	38	36	26	31	23	17	34
Number of fish							585	585	568	516	272	88	10	5	1

* Actual length at capture in November and December

† Age group not employed in computation of averages

‡ Beyond the fifth year of life the grand average calculated lengths were determined by the successive addition of the grand average annual increments of length to the grand average calculated length at the end of the fifth year

perch, it appears safe to state nevertheless that the discrepancies represent in the main real differences in the growth of the fish in the various age groups and not methodical errors traceable to the procedure followed in calculating growth. It can be stated also that the selective action of the fishing gear and selective destruction of the more rapidly growing individuals in the commercial fishery were doubtless among the most important factors contributing to the observed differences in the growth histories of the several age groups. Segregation according to size and maturity also may have played a significant rôle.

Rather large discrepancies occurred also between the corresponding calculated lengths of yellow perch that were members of the same age group but were collected in different calendar years. Perch of the 1932 collection, especially age groups IV and V, were large at capture and had large calculated lengths in the later years of life. This rapid growth of perch of the 1932 collection is believed to be in large measure the result of the use in that year of gill nets of mesh sizes greater than the 2½-inch mesh commonly employed by commercial fishermen in the Wisconsin waters of Green Bay. Evidence in support of the belief that nets with larger mesh sizes tend to select the larger fish may be found in Table VII, in which are shown the average lengths of some of the best-represented age groups as determined from the samples of gill nets of different mesh size.[2] Particular attention should be given to the data for the females, since males were represented so poorly that their average lengths were included only to show that the data for both sexes exhibited similar trends. With one exception the average length of the females of each age group increased with increase in the size of mesh. The differences between the average lengths of the age groups of females as determined from the sample of the 2½-inch-mesh net (approximately the equivalent of commercial gill nets) and as determined from the combined samples of all nets were: age group IV, 7 millimeters; age group V, 13 millimeters; and age group VI, 20 millimeters. The differences between the average lengths of female perch captured by 2½- and 2¾-inch-mesh gill nets were: age group IV, 21 millimeters;

[2] Since it was believed that only those collections should be employed that had been taken in nets of different mesh size fished simultaneously, a collection from Sturgeon Bay, for the capture of which only the 2¼-inch-mesh net was employed, was excluded in the preparation of Table VII.

TABLE VII

Relationship between the Mesh Size of the Gill Nets Employed in Taking the Samples and the Average Standard Length in Millimeters of the Representatives of Certain Age Groups in the 1932 Collection of Yellow Perch from Green Bay (Number of Specimens in Parentheses)

Mesh size (stretched measure in inches)	Length according to age group and sex					Average length of all perch taken in mesh *
	IV	V		VI		
	Female	Male	Female	Male	Female	
2⅜	188 (65)	201 (5)	191 (36)	197 (5)	191 (9)	190 (133)
2½	195 (31)	202 (7)	201 (36)	210 (7)	211 (19)	201 (106)
2⅝	206 (27)	220 (1)	211 (49)	207 (2)	211 (19)	207 (106)
2¾	209 (10)	202 (2)	215 (27)	227 (1)	218 (22)	210 (113)
Average	195 (133)	203 (15)	204 (148)	206 (15)	211 (69)	201 (458)

* Includes other age groups and 17 fish whose ages were not determined

age group V, 24 millimeters; and age group VI, 27 millimeters. From these data it is apparent that the selective action of fishing gear may have a pronounced effect on the determination of the growth histories of samples of fish.

Fluctuations in growth rate from one year to another also may have contributed to the discrepancies between the calculated growth of yellow perch of the same age group collected in different years.

In spite of the rather large discrepancies in the calculated growth histories of Green Bay yellow perch of the same and different ages, it is believed that a general growth curve based on the combination of the collections from all years and localities and taken by various types of gear provides a reasonably reliable index of the rate of growth of the population. The grand average calculated lengths and increments of length at the bottoms of Tables V and VI (see also Table XI for a direct comparison of the growth of the sexes and Figure 3 for a graphical representation of the growth of Green Bay perch) reveal that perch of both sexes made by far the greatest growth in length

in the first year of life. The much smaller growth increments of the later years exhibited a distinct although at times an irregular downward trend. (The males showed this trend more clearly than did the females.) Beginning in the third year of life the calculated lengths of females exceeded those of males. This sex difference ranged from 7 millimeters at the end of the third year to a maximum of 24 millimeters at the end of the seventh. The legal length of 7½ inches, total length (162 millimeters, standard length), was attained by the females in the latter part of the fourth year of life and by the males early in the fifth year of life. The ages at which lengths of 7, 8, and 8½ inches were reached were: 7 inches, in the fourth year of life of both the males and the females; 8 inches, at the end of the fourth year of life of the females and about the middle of the fifth year of life of the males; 8½ inches, about the middle of the fifth year of life of the females and at the end of the fifth year of life of the males.

The calculated weights of Green Bay yellow perch at the end of the different years of life (Table XII) correspond to the grand average calculated lengths, and were computed by means of the length weight equation given on page 257. The calculated weights of males and females were the same at the end of the first and second years of life. In later years the females had an advantage that varied from 7 grams at the end of the third year of life to 83 grams at the end of the seventh. The averages for the sexes reveal that the Green Bay perch did not reach a weight of a quarter pound until the fifth year of life. The weight of a half pound was reached in the seventh year of life, and the females weighed more than a pound in the ninth year.

Since records of sex were not available for the collections of yellow perch from Lake Michigan, the discrepancies among the calculated lengths of the age groups (Table VIII) may depend in part on variations in the relative abundance of males and females at different ages. Other factors, mentioned previously, also doubtless contributed to the occurrence of Lee's phenomenon in the growth data for Lake Michigan perch. In spite of the lack of sex records the data of Table XI indicate conclusively that Green Bay fishermen are in error in their contention that perch grow more slowly in Green Bay than in Lake Michigan. The grand average calculated lengths of the Lake Michigan perch were well below the calculated lengths of female Green Bay perch in all years of life beyond the first and were

less than the calculated lengths of male Green Bay perch in every year of life but the sixth. The slow growth of perch in the samples from Lake Michigan cannot well be attributed to the selective action of gear since they were taken by gill nets of relatively large mesh ($2\frac{5}{8}$ inches, stretched measure).

The calculated growth in weight of Lake Michigan yellow perch (Table XII) was computed by means of the length–weight equation given on page 257. By reason of their more robust form their cal-

TABLE VIII

AVERAGE LENGTH AND WEIGHT AT CAPTURE OF YELLOW PERCH COLLECTED IN NORTHERN LAKE MICHIGAN IN SEPTEMBER, 1937, AND THE AVERAGE CALCULATED LENGTH ATTAINED BY THE AGE GROUPS AT THE END OF EACH YEAR OF LIFE (NO RECORDS OF SEX OBTAINED)

Age group	Number of fish	Weight in ounces	Total length in inches	Weight in grams	Standard length in millimeters	Calculated standard length in millimeters at end of year of life					
						1	2	3	4	5	6
VI	8	9.5	10.4	269	225	56	83	113	148	172	201
V	27	5.7	8.9	161	193	58	87	110	136	166	..
IV	118	5.6	8.9	158	193	61	92	118	159	..	..
III	98	5.1	8.6	144	187	61	99	145	..	..	..
II	25	4.2	8.2	120	177	64	116	..	..	..	..
Grand average calculated length*						61	96	128	154	183	212
Annual increment of length						61	35	32	26	29	29
Number of fish						276	276	251	153	35	8

* Beyond the fourth year of life the grand average calculated lengths were determined by the successive addition of the grand average annual increments of length to the grand average calculated length at the end of the fourth year

culated weights exceeded those of Green Bay perch in four of the six years of life for which comparisons were possible, and were equal to or only slightly less than the weights of Green Bay fish in the remaining two years of life.

The data for a number of selected large yellow perch from Green Bay and Lake Michigan provide some idea of the maximum size and age attained in those areas. The largest perch captured in Green Bay was a female with a total length of 14.3 inches (311 millimeters, standard length) and a weight of 26 ounces (737 grams).

This fish, which was taken one-half mile south of Marinette, was a member of age group VII. There is no record of the gear in which the fish was captured. The biological samples from Green Bay included a number of older fish but none so large. The largest perch from Lake Michigan were three females taken off Bailey's Harbor in $4\frac{1}{2}$-inch-mesh gill nets on March 29, 1938. At capture each weighed 28 ounces (794 grams). The ages, total lengths in inches, and standard lengths in millimeters were as follows: age group VI, 13.8 inches, 300 millimeters; age group VII, 13.5 inches, 294 millimeters; age group IX, 14.3 inches, 311 millimeters.

TABLE IX

Ratio of Standard Length to Total Length of Yellow Perch from Green Bay and the Beaver Island Region of Lake Michigan

Interval of standard length in millimeters	*Ratio of standard length to total length*	*Number of fish*
149 and less	0.844	57
150–209	0.853	657
210 and more	0.858	155

In the preceding discussion corresponding total and standard lengths have been presented without a statement of the relationship between the two. Measurements of 869 yellow perch made possible the determination of the ratios of standard length to total length in fish of different sizes (Table IX).

LENGTH–WEIGHT RELATIONSHIP

Although the length–weight data of Green Bay yellow perch were tabulated originally according to sex and year of capture, the variation from year to year in the length distribution of the samples and the scarcity of males in some collections made a detailed analysis unfeasible. Data presented here will be limited to the general length–weight curve based on a combination of all available materials. It may be stated, however, that the Green Bay perch tended to be heaviest in relation to their length in 1937 and lightest in 1934. Females were heavier than males of corresponding length in 1932 and 1938, but were lighter in 1934. Sex differences were negligible in 1937. In the combined collections females averaged slightly heav-

ier than males (average coefficient of condition,[3] K, of 1.85 as compared with a coefficient of 1.81 for males over the length intervals in which both sexes were represented).

The lack of sex records for all but a few selected individuals of the Lake Michigan collections prevented the determination of possible sex differences in the length–weight relationship of yellow perch from that area.

The comparison of weights and coefficients of condition of yellow perch from Green Bay and Lake Michigan by centimeter intervals of standard length (Table X) reveals that the Lake Michigan fish were much the heavier at the lengths represented by adequate numbers of individuals. This advantage is reflected also in the higher grand average K (2.18 in Lake Michigan; 1.87 in Green Bay). To some extent their greater weights may be held to represent real differences between the populations, although seasonal and annual fluctuations in the length–weight relationship may also have played a rôle.

The coefficients of condition of Green Bay yellow perch tended to increase with increase in length up to a length of 180 millimeters. This increase was followed by a decline over the interval, 180–219 millimeters, and an increase beyond the latter length. In the Lake Michigan perch the values of K tended to decline with increase in length among the smaller fish, but were extremely high at the greatest lengths.

The fitting of parabolas to the length–weight data[4] yielded the following equations:

$$\text{Green Bay, } W = 0.9319 \times 10^{-5} L^{3.133}$$
$$\text{Lake Michigan, } W = 5.8405 \times 10^{-5} L^{2.811}$$

In both equations W = weight in grams and L = length in millimeters.

The solutions of these equations are represented graphically by the smooth curves of Figure 2. Comparisons with the empirical data reveal fairly good agreement within the intervals over which the equations were fitted. The weights of the longer fish from both

[3] $K = \frac{W \times 10^5}{L^3}$, where W = weight in grams and L = length in millimeters.

[4] The equations were fitted to the average lengths and weights by five-millimeter intervals of standard length.

TABLE X

LENGTH–WEIGHT RELATIONSHIP OF YELLOW PERCH FROM GREEN BAY AND LAKE MICHIGAN

Interval of standard length in millimeters	Total length in inches equivalent to mid-point	Green Bay				Lake Michigan			
		Weight in grams	Weight in ounces	*K*	Number of fish	Weight in grams	Weight in ounces	*K*	Number of fish
100–109	4.9	19	0.7	1.62	10	...	...	...	...
110–119	5.3	25	0.9	1.63	22	...	...	...	...
120–129	5.8	34	1.2	1.74	39	...	...	...	...
130–139	6.3	45	1.6	1.81	33	...	...	...	...
140–149	6.7	58	2.0	1.88	44	...	...	...	...
150–159	7.1	71	2.5	1.92	83	96	3.4	2.48	3
160–169	7.6	84	3.0	1.91	100	104	3.7	2.30	14
170–179	8.0	105	3.7	1.95	91	121	4.3	2.23	70
180–189	8.5	120	4.2	1.89	106	138	4.9	2.15	84
190–199	9.0	136	4.8	1.84	110	157	5.5	2.11	50
200–209	9.4	157	5.5	1.84	117	181	6.4	2.14	44
210–219	9.8	178	6.3	1.83	95	214	7.5	2.17	11
220–229	10.3	207	7.3	1.85	43	261	9.2	2.26	9
230–239	10.8	240	8.5	1.90	20	...	...	...	...
240–249	11.2	288	10.2	2.04	10	295	10.4	2.01	1
250–259	11.7	370	13.1	2.34	2	391	13.8	2.28	3
260–269	12.1	406	14.3	2.18	4	...	...	...	...
270–279	12.6	436	15.4	2.13	2	...	...	...	...
280–289	13.1	624	22.0	2.67	2	473	16.7	2.02	1
290–299	13.5	652	23.0	2.57	2	709	25.0	2.79	2
300–309	14.0	598	21.1	2.14	2	794	28.0	2.94	1
310–319	14.4	737	26.0	2.45	1	794	28.0	2.64	1
Average or total	...	...	...	1.87	938	...	...	2.18	294

Green Bay and Lake Michigan were far greater than those computed from the length–weight equations.

At the attainment of Wisconsin's legal length (7½ inches, total length; 162 millimeters, standard length) Green Bay yellow perch had a weight of 2.8 ounces (78 grams) and Lake Michigan perch a weight of 3.4 ounces (95 grams). The weights at 7, 8, and 8½ inches were 2.3, 3.4, and 4.1 ounces, respectively, in Green Bay and 2.8, 4.0, and 4.8 ounces in Lake Michigan. The advantages of the Lake Michigan perch at the three lengths were 0.5, 0.6, and 0.7 ounces.

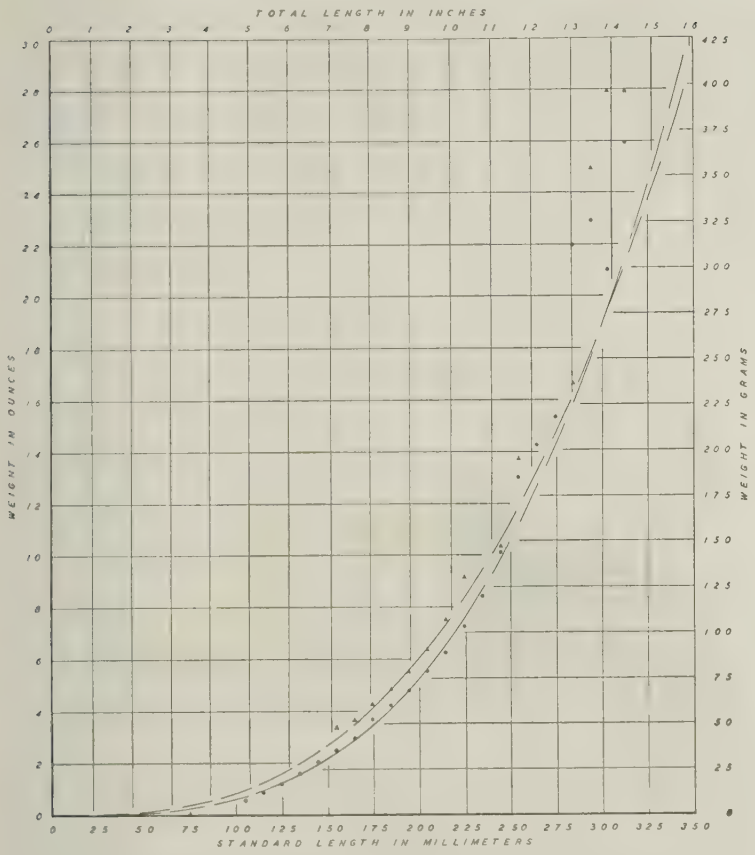

FIG. 2. Length–weight relationship of yellow perch (sexes combined) from Green Bay (circles) and northern Lake Michigan (triangles). The solid-line portions of the curves represent the range of lengths to which the equations were fitted

SIZE AT MATURITY AND SEX RATIO

Records of the state of maturity were obtained for the Green Bay yellow perch of the 1932 and 1934 collections. (The data on sexual maturity are based on 50 fish from bait nets of $1\frac{3}{8}$-inch-mesh, 17 fish not aged in 1932, and 4 not aged in 1934, in addition to the

collections listed in Table I for 1932 and 1934.) Practically all the males (128 in a total of 133) and 85.0 per cent of the females (413 in a total of 486) were mature. Males were predominantly mature down to a total length of 5 inches. A majority of the females were immature at all lengths below 7 inches. More than half (58.8 per cent) were mature at 7 to 7½ inches, and nearly all were mature above the length of 7½ inches. It cannot be concluded, however, that most female Green Bay perch become mature at 7½ inches, since the samples were taken during the spawning run in 1932 and shortly before the spawning run in 1934. Spawning-run samples tend to be made up almost entirely of mature fish. Unpublished data on the Lake Erie perch have demonstrated that the percentage of mature individuals at the lower lengths was much higher in spawning-run samples than in samples taken at other seasons. These Lake Erie data suggest that the length at which a majority of female Green Bay perch are mature is most probably greater than 7 to 7½ inches.

The data on the relative abundance of the sexes in samples of Green Bay yellow perch were extremely variable. The number of females per 100 males ranged from 114 in 1934 to 688 in 1932 and was 356 for the collections of all the years combined. The change of the sex ratio with increase in age varied also. Males tended to become more abundant with increase in age in 1932 (a spring collection) and 1937 (a fall collection). No distinct trend was apparent in the data for the 1934 and 1938 collections (both taken in the spring). The data on the sex ratio of the Green Bay perch lend further support to the growing belief that the sexes may be segregated throughout much of the year.

COMPARISON OF THE GROWTH OF YELLOW PERCH IN GREEN BAY AND NORTHERN LAKE MICHIGAN WITH GROWTH IN LAKE ERIE AND SAGINAW BAY

Studies have been made of the age and growth of the Lake Erie yellow perch by Jobes (MS) and of the Saginaw Bay yellow perch by Hile and Jobes (see note 1). The data of Tables XI and XII and Figures 3 and 4 permit a comparison of the growth of perch in length and weight in four Great Lakes regions.

The calculated lengths of Lake Erie yellow perch were considerably greater than those of yellow perch from other areas of the Great Lakes during the first three years of life. The advantage of Lake

TABLE XI

Comparison of Growth in Length of Yellow Perch from Four Areas of the Great Lakes

Locality	Sex	Calculated standard length in millimeters at end of year of life								
		1	2	3	4	5	6	7	8	9
Lake Erie.....	Male	76	143	181	203	220	...	...	...	...
	Female	77	146	187	215	234	251	...	...	...
	Both*	76	144	184	209	227	...	...	...	...
Saginaw Bay.....	Male	65	114	166	204	232	259	275	...	...
	Female	65	116	174	211	236	270	293	...	...
	Both*	65	115	170	208	234	265	284	...	...
Green Bay.....	Male	62	99	130	159	185	211	227	...	...
	Female	61	99	137	173	197	228	251	268	302
	Both*	61	99	134	166	191	220	239	...	...
Northwestern Lake Michigan....	Both	61	96	128	154	183	212	...	...	...

* Unweighted mean

Erie perch over fish from Saginaw Bay was reduced from a maximum of 29 millimeters in the second year to 14 millimeters in the third and 1 millimeter in the fourth. At the end of the fifth year the Saginaw Bay perch were 7 millimeters longer than the Lake Erie fish. Comparisons of the calculated lengths of perch from Lake Erie and Green Bay reveal that the advantage of the Lake Erie perch increased from 15 millimeters at the end of the first year to a maximum of 50 millimeters at the end of the third and then declined to 36 millimeters at the end of the fifth year. The advantage of the Saginaw Bay perch over fish from Green Bay increased from 4 millimeters at the end of the first year to 45 millimeters at the end of the sixth and seventh years of life. The Green Bay fishermen seem to be correct in their belief that perch grow relatively slowly in the bay, although their belief that they grow more slowly in Green Bay than in Lake Michigan is in error. The calculated lengths of Lake Michigan perch were less than the lengths of Green Bay fish in all but the first year. The greatest difference (12 millimeters) occurred in the fourth year.

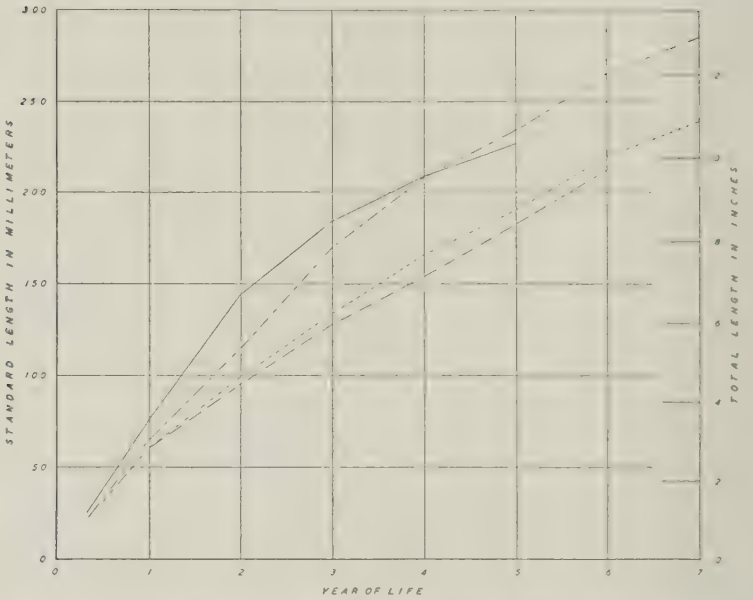

FIG. 3. Calculated growth in length of yellow perch (sexes combined : Lake Erie, ——; Saginaw Bay, – – –; Green Bay, – – –; Lake Michigan, ———

The legal length of $8\frac{1}{2}$ inches, total length,[5] was attained by the Lake Erie yellow perch in approximately three years and by the Saginaw Bay fish during the fourth growing season. The Wisconsin size limit of $7\frac{1}{2}$ inches, total length, was reached toward the latter part of the fourth growing season in Green Bay and in the early part of the fifth in Lake Michigan. In these two localities approximately five years were required for the attainment of the length of $8\frac{1}{2}$ inches, the size limit in Lake Erie and Saginaw Bay. On the other hand, Lake Erie perch reached a length of $7\frac{1}{2}$ inches, the size limit in the Wisconsin waters of Green Bay and Lake Michigan, at about the middle of the third growing season, and Saginaw Bay perch attained that length near the end of the third growing season.

[5] Factors for conversions between standard and total length were slightly different in Lake Erie, Saginaw Bay, and Green Bay and Lake Michigan. The total lengths shown in Figure 3 corresponding to the various standard lengths are the averages of the values determined separately for fish of each of the three areas.

TABLE XII

COMPARISON OF THE GROWTH IN WEIGHT OF YELLOW PERCH FROM FOUR AREAS OF THE GREAT LAKES

The calculated weights correspond to the calculated lengths of Table XI.

Locality	Sex	Calculated weight in grams at end of year of life								
		1	2	3	4	5	6	7	8	9
Lake Erie	Male	8	56	113	160	204	...	...	...	...
	Female	9	59	125	190	246	303	...	...	...
	Both *	8	57	119	175	225	...	...	...	...
Saginaw Bay	Male	4	25	82	156	233	328	395	...	...
	Female	4	27	95	173	245	373	482	...	...
	Both *	4	26	89	165	239	351	439	...	...
Green Bay	Male	4	17	39	73	118	178	224	...	...
	Female	4	17	46	96	144	227	307	377	548
	Both *	4	17	43	85	131	203	266	...	...
Northwestern Lake Michigan	Both	6	22	49	83	134	203	...	...	...

* Unweighted mean

With respect to weight as well as length Lake Erie yellow perch were larger than yellow perch from Saginaw Bay during the first four years of life, but were smaller at the end of the fifth year. The greatest difference (31 grams) occurred at the end of the second year. The difference between the calculated weights of perch from Lake Erie and Green Bay increased progressively from 4 grams at the end of the first year of life to 94 grams at the end of the fifth year. Perch from Saginaw Bay and Green Bay had the same calculated weights at the end of the first year. In later years, however, the Saginaw Bay fish had an advantage ranging from 9 grams at the end of the second year of life to 173 grams at the end of the seventh. As mentioned previously (p. 255), the advantage of Green Bay perch over Lake Michigan perch with respect to growth in length did not include growth in weight. This difference with respect to growth in length and weight is to be explained by the fact that the yellow perch of the Lake Michigan population averaged somewhat heavier than the Green Bay fish of corresponding length.

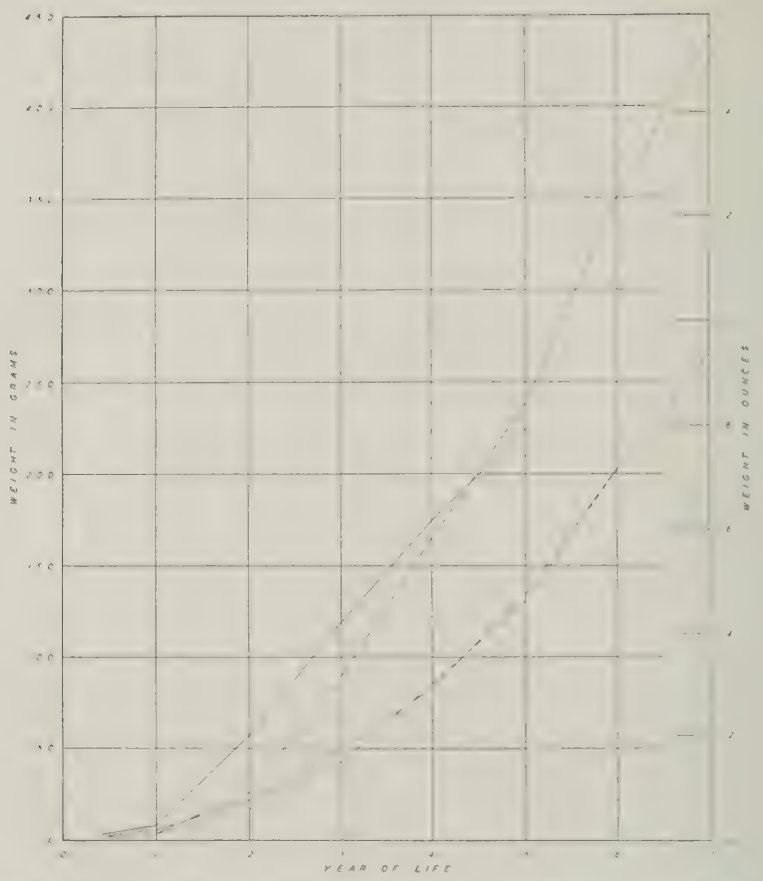

FIG. 4. Calculated growth in weight of yellow perch (sexes combined): Lake Erie, ——; Saginaw Bay, ——-; Green Bay, -----; Lake Michigan, ———

SUMMARY

1. Ages of yellow perch were determined and individual growth histories were computed from the examination and measurement of the scales of 752 fish collected in 1932, 1934, 1937, and 1938 from the Wisconsin waters of Green Bay, and of 276 yellow perch taken from the Wisconsin waters of northern Lake Michigan in 1937. In

addition, ages were determined for 90 Green Bay perch for which sex records were lacking and for 9 large fish, selected for size, from both Green Bay and Lake Michigan. Sex records were lacking for all Lake Michigan perch except the large, selected individuals.

2. The numbers of fish employed for other phases of the investigation were: length weight relationship, 938 from Green Bay and 294 from Lake Michigan; relationship between total length and standard length, 869 collected in Green Bay and northeastern Lake Michigan.

3. Samples of the commercial catch of Green Bay yellow perch were dominated by age groups II, III, and IV. Samples taken by experimental gill nets with mesh sizes larger than those employed in the commercial fishery were dominated by age group V. The collections from Lake Michigan were dominated by age group IV.

4. The length frequency distributions of the age groups of Green Bay yellow perch exhibited extensive overlap. A majority of the females had reached the legal size of $7\frac{1}{2}$ inches, total length, at the end of four growing seasons, but a majority of the males did not attain this length till during the fifth year. In the combined samples from the catch of commercial gear 30.8 per cent of the perch were below the legal length of $7\frac{1}{2}$ inches. The samples from Lake Michigan contained only four (1.4 per cent) yellow perch less than $7\frac{1}{2}$ inches long.

5. The calculated growth histories of the age groups revealed some rather large discrepancies in the corresponding computed lengths of yellow perch of the same and different ages. The probable factors contributing to these discrepancies were mentioned briefly.

6. The general growth data showed that yellow perch of both sexes made by far the greatest growth in length during the first year of life. The growth increments of the later years exhibited a distinct although an irregular tendency to decrease. In the third and later years of life the grand average calculated lengths of females were larger than the corresponding lengths of males.

7. Green Bay fishermen are in error in their belief that yellow perch grow more rapidly in Lake Michigan than in the bay. The grand average calculated lengths of Lake Michigan perch (sexes combined) were less than the corresponding lengths of female perch from Green Bay in all but the first year of life and less than the corresponding lengths of male perch from Green Bay in all but the sixth year. Perch from Green Bay attained the legal length of $7\frac{1}{2}$

inches late in the fourth growing season; those from Lake Michigan, in the fifth season.

8. The calculated weights of Lake Michigan yellow perch tended to be slightly greater than those of Green Bay perch in corresponding years of life in spite of the slower growth in length of the Lake Michigan population.

9. The relationship between the length (L) of Green Bay yellow perch in millimeters and the weight (W) in grams was $W = 0.9319 \times 10^{-5} L^{3.133}$. The length–weight equation for Lake Michigan yellow perch was $W = 5.8405 \times 10^{-5} L^{2.811}$. In both populations the weights of the larger perch (beyond the length intervals over which the equations were fitted) tended to be higher than the weights computed from the equations. Lake Michigan perch almost always were heavier than Green Bay fish of corresponding length.

10. In samples taken immediately before and during the spawning run a majority of the male Green Bay yellow perch were mature down to a length of 5 inches and a majority of the females were mature at 7 to 7½ inches. Spawning-run samples, however, tend to contain only mature fish; collections taken at other seasons probably would first show a majority of mature females at a length somewhat greater than 7 to 7½ inches.

11. The sex ratio of yellow perch in the collections of the different years from Green Bay ranged from 114 females per 100 males in 1934 to 688 females per 100 males in 1932. The relative abundance of males tended to increase with increase in age in 1932 and 1937. In 1934 and 1938 no consistent changes were noted in the sex ratio with increase in age.

12. Comparisons of the calculated growth in length and weight of yellow perch from Lake Erie, Saginaw Bay, Green Bay, and northern Lake Michigan showed the Lake Erie perch to be the longest and heaviest during the first four years of life. At the end of the fifth year Saginaw Bay perch were longer and heavier than the Lake Erie fish. The growth of Green Bay perch was distinctly inferior to growth in Lake Erie and Saginaw Bay. Lake Michigan perch grew somewhat more slowly than the Green Bay perch in length but not in weight.

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HYBRIDIZATION IN NATURE BETWEEN TWO GENERA OF FLOUNDERS IN JAPAN

CARL L. HUBBS AND KATSUZO KURONUMA

A CONSIDERABLE number of naturally produced interspecific fish hybrids, with characters almost uniformly intermediate between those of the parental species, have been described, and more are constantly being discovered (Hubbs, 1940 : 205–209). The great majority of these hybrids are between fresh-water species, particularly of the families Cyprinidae (a large literature) and Centrarchidae (see particularly Hubbs and Hubbs, 1933, and Bailey and Lagler, 1938). Among marine fishes natural hybrids are much less frequent — perhaps because the ecological niches and the communities are more varied and less ephemeral.

The flatfishes (Heterosomata) of the families Bothidae and Pleuronectidae, however, resemble the fresh-water fishes in the frequency of hybridization between species which are so distinct as to warrant reference to separate genera. This is in line with ecological expectation. It is well known, as the result of many faunal surveys and a plethora of fisheries research, that in most northern regions several species of flounders often commingle in abundance over rather uni form habitats of sand and mud bottom, in shallow to moderate depths. The breeding seasons tend to be rather long, and are synchronous or overlapping for the different species. Reproductive habits are generalized; it is assumed that the pelagic eggs are fertilized as they start their ascent toward the surface. The wonder is that interspecific hybrids among the flounders are not more frequent.

Most of the known flatfish hybrids have naturally been described from European waters. The rather extensive literature, cited by Norman (1934 : 266–267, 336, 354–355, 366, figs. 205, 258), refers to the following crosses:

Psetta maxima × *Scophthalmus rhombus*
Limanda limanda × *Platichthys flesus*
Platichthys flesus × *Pleuronectes platessa*
Limanda limanda × *Pleuronectes platessa*
Glyptocephalus cynoglossus × *Pleuronectes platessa*

Apparently Norman did not mention, and perhaps did not accept, Krause's (1881) description of one fish as a hybrid between *Platessa vulgaris* and *Rhombus maximus* (= *Pleuronectes platessa* × *Psetta maxima*) — in current taxonomy an interfamily as well as an intergeneric cross. The rather well known hybrid between turbot and brill (*Psetta maxima* × *Scophthalmus rhombus*) was experimentally produced by McIntosh (1893 : 318–319, pl. 4; see also McIntosh and Masterman, 1897 : 338–340, pl. 13 fig. 7). Kyle (1903 : 623–625) referred to the same studies, and recounted experiments on the production of embryos of the other relatively frequent and well-authenticated European flatfish hybrid, *Platichthys flesus* × *Pleuronectes platessa*. That combination has recently been treated in commendable detail by Kändler (1935; 1936) and Pape (1936). In reporting a possible hybrid between diverse genera of soles (*Austroglossus* × *Synaptura*) Chabanaud (1937) has extended the literature on hybrid flatfishes systematically to the solaeiform Heterosomata, and geographically to Africa and the Southern Hemisphere. There has been only one report (Nichols, 1918) of a hybrid flounder from the western Atlantic, but this specimen, on reëxamination by Hubbs and Carrick (MS), has been interpreted as a teratological winter flounder (*Pseudopleuronectes americanus*) rather than as a hybrid between that species and *Limanda ferruginea*.

To date only one interspecific hybrid combination has been indicated in the flatfish group for the Pacific Ocean. Schultz and Smith (1936) and Herald (1941) have convincingly shown that the rare flounder of western North America called *Inopsetta ischyra* is an intergeneric hybrid. *Platichthys stellatus* is obviously one parental species (as the senior author of the present paper has thought for years). Norman (1934 : 375–376, fig. 271) and Schultz and DeLacy (1936 : 68) suggested that this flounder might be a hybrid between *Lepidopsetta bilineata* and *Platichthys stellatus*, but the analysis by Schultz and Smith points definitely to *Parophrys vetulus* as the other parent species.

The published information on interspecific hybrids within the Pleuronectidae may be summarized as follows: Four combinations are reported to occur in European waters (the *Psetta* × *Scophthalmus* cross is within the Bothidae) and one on the Pacific Coast of North America. We regard all these hybrids as intergeneric. Some evidence for the hybrid interpretation has been furnished by the

experimental production of embryos of two combinations, but the best evidence is circumstantial. In view of the very extensive flounder fisheries which have yielded all the presumed hybrids one can feel confident that these forms are too rare and too sporadic in occurrence to represent self-perpetuating species. A large number of circumstances, involving habitat selection, spawning seasons, and general behavior, favor their interpretation as interspecific crosses. The genetic evidence is that the characters all tend to be intermediate between those of the assumed parent species, and often variably intermediate. In all these respects they conform with the general rules regarding interspecific fish hybrids (Hubbs, 1940 : 205 209), including the combinations which have been clinchingly demonstrated by experiment.

Another observation of interest in connection with the new flatfish hybrid combination described in this paper is that two of the four European pleuronectid hybrids involve *Platichthys* as one of the parental genera, and the one other accepted combination in the family is between *Platichthys stellatus* and another genus and species. In other groups, too (as in Cyprinidae and Centrarchidae), certain forms are particularly wont to hybridize with other species.

KAREIUS BICOLORATUS × *PLATICHTHYS STELLATUS*

During his field studies of 1929 in Japan the senior author discovered that *Platichthys stellatus* hybridizes with a related flounder, *Kareius bicoloratus*. Since that time Hikita (1934 : 11 15, of English section, and pl. 2), on the basis of two specimens collected by him at Oshoro, Hokkaido, has described this hybrid under the new generic and specific name, *Pseudoplatichthys oshorensis*. Hikita's description and his plate, which beautifully portrays a male and a female adult in color, correspond in all essential respects with the specimens which we have studied. Hikita's statement of the relationships of the nominal genus and species is as follows:

> This new species is allied to *Kareius bicoloratus* and *Platichthys stellatus*, but differs from the former in the following characters; cranium, clavicle, interclavicle, first interhaemal spine and otolith larger in size; two lower pharyngeal bones separated (a deltoid bone in *K. bicoloratus*); vertical fins with many black bars and body with stellated tubercles (horny plates in *K. bicoloratus*); and from the latter, body dextral (sinistral in *P. stellatus*); much more bony prominence on cranium; vertical fins with comparatively indistinct black bars and fewer stellate tubercles on body.

The evidence for interpreting these fish as hybrids is again circumstantial, but quite convincing in our view. All the pertinent information which we have been able to derive from our own field and museum studies and from published observations harmonizes with this interpretation.

The Distribution, Habitat, and Spawning Season of the Parental Species

Platichthys stellatus and *Kareius bicoloratus* overlap widely in their geographical distribution (Fig. 1), as was well demonstrated by the senior author in 1929, when he made frequent collections along both coasts of Japan. The Pacific species of *Platichthys* ranges from the outer coast of Santa Barbara County in Southern California to the Bering Strait region of Alaska, and thence eastward to Coronation Gulf near the middle of the Arctic coast of Canada; also along the Aleutian Archipelago to the Commander Islands, and southward from the eastern coast of Kamchatka and the entire Okhotsk Sea to central Japan. It is not clear from the statements of Andriashev (1939: 48, 72, 181) whether the species ranges northward on the west side of Bering Sea to Cape Navarin and the southern part of the Gulf of Anadyr. The southern limits in Asia appear to be as follows: on the mainland, the vicinity of Gensan, in mid-eastern Korea (Chosen); on the west coast of Honshyû, the Noto Peninsula; and on the Pacific side of Japan, probably no farther than Kasumiga-ura (Okada and Ikeda, 1938: 120; we suppose that the extension of the range to Tokyo, as given by Soldatov and Lindberg, 1930: 410, and Norman, 1934: 384, was based on Tokyo market specimens shipped from farther north). *Kareius bicoloratus* is confined to Asia, and inhabits the shore waters from the Kurile Islands (Chishima), southern Sakhalin (Karafuto), and Peter the Great Bay (Taranetz, 1938: 121, 129, fig. 5), southward to the Inland Sea along the Pacific coast, to northern Kyûshyû along the eastern side of the Sea of Japan; and on the mainland through the Yellow Sea to the southern shore of the Shantung Peninsula in China. The overlap in distribution along the eastern coast of the Sea of Japan is thus about 10° of latitude, and is nearly as much on the two other coast lines of Japan.

The several localities in Japan where the hybrids were secured (Fig. 2) lie within the area in which the ranges of the two parental

FIG. 1. Map showing the overlapping distribution of *Kareius bicoloratus* and *Platichthys stellatus*

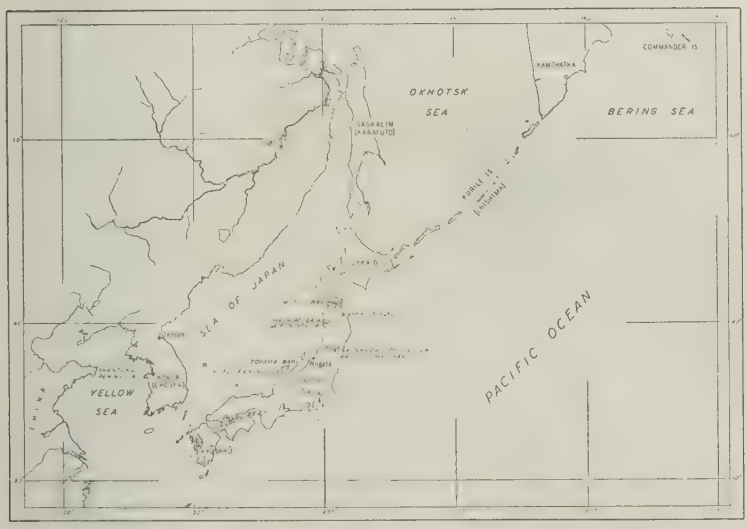

FIG. 2. Asiatic localities mentioned in the chart, including those where the interspecific hybrids were secured

species overlap. Following is a list of the record stations and of the hybrid material obtained:

Oshoro, Hokkaido: two adult hybrids (reported by Hikita, 1934). *Platichthys* and *Kareius* occur in this region. The former is common

along the Hokkaido coast, and in 1929 Professor Hikita collected a specimen of *Kareius* at Oshoro for the senior writer.

Matsushima Bay (collection secured in the fish markets at Sendai and Shiogama, September 3–7, 1929; field number, H29–295a): one hybrid 236 mm. in standard length, collected with five specimens of *Kareius* and one of *Platichthys*.

Off Kinkazan (collection obtained in the markets of Shiogama and Sendai, September 3–7, 1929; field number H29 295b): 15 hybrids, 191 to 357 mm. long, taken with 10 specimens of *Kareius* (all preserved) and 7 examples of *Platichthys*. In addition, 370 other in-

TABLE I

Size Groups of Japanese Specimens of Hybrid Flounders and of the Parental Species

	Standard length in millimeters									No.
	0–49	50–99	100–149	150–199	200–249	250–299	300–349	350–399	400–449	
Kareius bicoloratus	2	19	11	36	11	2	..	2	..	83
Hybrid	1	1	1	6	6	4	4	1	1	25
Platichthys stellatus	2	6	15	26	9	5	2	..	..	65

dividuals of *Platichthys* were examined fresh to determine that the left side of all carried the eyes and color, that stellate prickles were constantly developed on the eyed side (though they varied much in size and number), and that all had stellate prickles along virtually the entire length of the dorsal fin base. All but one of the fifteen hybrids were found on the dock market at Shiogama as the fish were being unloaded from small craft, which had been fishing with *teguri-ami* (a type of trawl). Japanese helpers (zoology assistants of Tohoku Imperial University, kindly furnished by Professor Shinkishi Hatai) asked each crew where they had made their catch, and we thus learned that almost all boats fishing at depths of 20 to 25 fathoms had caught at least one hybrid. It was therefore obvious that the hybrids were relatively common and well distributed over the trawling ground off Kinkazan. The hybrid specimens varied widely in size (from 191 to 357 mm. in standard length; see also Table I, for the size classes of the specimens preserved), and surely represented more than one age group. Therefore the seventeen hybrids taken

in this region in five days cannot be attributed to a single brood and are probably not the result of any very local production.

Off Kinkazan (collection obtained in the markets of Shiogama and Sendai, September 3–7, 1929; field number H29 295c): one large adult hybrid, 427 mm. long, taken with three adults of *Kareius* but none of *Platichthys*. This series was collected by the *teguri-ami* boats at a greater depth (about 60 fathoms), perhaps beyond the ordinary bathymetric limits of *Platichthys stellatus*, which throughout its range is essentially an inshore, more or less estuarine fish.

Hachirô-gata, a large brackish lake in Akita-ken, near the coast of the Sea of Japan (sample taken in the Akita fish market, August 21–22, 1929; field number H29–260): one small specimen, of 58 mm., taken with eleven specimens of *Platichthys* but none of *Kareius* (both genera, however, are included in a collection secured at the same time from a trawl fishery operating near by in the Sea of Japan in about 25–80 fathoms, between Henashi-zaki and Oga Peninsula). This hybrid specimen, like the others listed below, was not recognized as such in the field.

Hachirô-gata, at Funagoshi (collection obtained July 5, 1929, and presented to the senior author by the Tsuchizaki Fisheries Experiment Station; field number H29 262): one young hybrid, 35 mm. long. Apparently the young hybrids tend to follow *Platichthys* into the brackish waters (the young of *Platichthys* often live in fresh water, as do the adults occasionally, even where it is rapidly flowing near the mouths of creeks and rivers). The young of *Kareius* would seem to be more rigidly restricted to salt water.

Sea of Japan, close to Niigata (these fish were found in the Niigata market August 18–20, 1929, but inquiry was made as to their source; field number H29–255): four hybrids, 147 to 171 mm. long, preserved with eleven specimens of similar size of *Platichthys* and one of *Kareius* (the ratio of specimens is not significant, since these hybrids were not distinguished in the field).

Two additional hybrids, 234 and 240 mm. long, are in the Chosen Fisheries Experimental Station at Fusan. They were collected by the late Dr. Yojiro Wakiya "somewhere in Japan," and have been studied in Japan by the junior author. One of these was reported as *Platichthys stellatus* (Anonymous, 1936).

During the collecting in 1929 *Kareius* and *Platichthys* were taken together, but without hybrids, in the harbor at Same-Minato, and

on the Pacific coast of Aomori-ken, both near the northern end of Honshyû. Both genera were also captured, though not in identical collections, in Toyama Bay in the vicinity of Namerikawa, and along the shore of Noto Peninsula. These Japanese localities are indicated on our map (Fig. 2).

It is evident from the field data that there is an overlap between the ecological as well as the geographical ranges of *Platichthys stellatus* and *Kareius bicoloratus*. There are indications that the large hybrids descend offshore to depths greater than those inhabited by *Platichthys*, and that the young ones enter brackish waters which seem to be shunned by *Kareius*. All *Kareius* × *Platichthys* specimens, however, were taken in habitats occupied by at least one of the parental species.

Furthermore, there appears to be no temporal barrier to hybridization between *Kareius bicoloratus* and *Platichthys stellatus*. According to the researches of Hikita (1934), the spawning season of the two genera (February and March) coincides in the waters of Hokkaido. Adult males and females of both species, taken with 17 hybrids in the vicinity of Matsushima Bay and Kinkazan on September 3–7, have well-developed gonads, ripened to approximately the same degree. Unfortunately there are almost no available data on the precise spawning habits of either parental species.

Possible Partial Fertility of the Hybrids

The well-developed gonads, the even sex ratio (1 male to 1 female in Hikita's series of two, and 11 males to 12 females in the twenty-three half-grown to adult hybrids at hand), and the variable intermediacy of the characters as shown below, all suggest that the *Kareius* × *Platichthys* hybrids may be at least partly fertile. The indications that one specimen may represent a backcross with *Platichthys* checks with this idea.

Taxonomic Relationship between Parental Species

It seems obvious that we are dealing with an interspecific hybrid, for no ichthyologist would deny that *Kareius bicoloratus* and *Platichthys stellatus* are distinct. These species differ in matters of kind as well as degree, and the differences pervade them throughout; in the sense of Goldschmidt (1940) they are "good species," with distinct "reaction systems." Whether we have before us an inter-

generic as well as an interspecific hybrid is, of course, a question that involves taxonomic judgment. In his excellent systematic revision of the flounders Norman (1934:376) has combined *Karcius* with *Platichthys*, and hence in his view the hybrid under treatment is only interspecific. We prefer, however, to maintain *Karcius* Jordan and Snyder (1900:379) as a distinct genus—closely related to *Platichthys*, to be sure, but perhaps, as most recent authors have indicated, with a relationship quite as close to *Liopsetta*. In maintaining *Karcius* as a separate genus we agree with the systematic decision expressed in the treatises by Schmidt (1904:243–244), Jordan and Starks (1906:220–221), Tanaka (1913:192–195, pl. 52, fig. 198), Hubbs (1915:488), Jordan and Hubbs (1925:300), Soldatov and Lindberg (1930:410), Wu (1932:10–13, 17, 31, 33, 37–38, 42, 44, 55–56, 62–64, 71, 116–118, figs. 1–3, 25); Hikita (1934:10, 193–197, pl. 3, fig. 5, and pl. 10), Okada, Uchida, and Matsubara (1935:242, pl. 142, fig. 3), Taranetz (1938:121, 129, fig. 5), and all other recent ichthyologists who have specialized in the study of Japanese and Chinese fishes.

That *Karcius bicoloratus* possesses very distinctive characters has been demonstrated by the authors just cited, and also by Steindachner (1870b:628–629, pl. 2), in his detailed description of *Pleuronectes scutifer*. The treatment by Wu is particularly thorough. Most of the authors cited have indicated by their descriptions, if not by direct comparisons, that *Karcius bicoloratus* differs sharply from *Platichthys stellatus*. Excellent figures of Asiatic specimens of *Platichthys* were included by Soldatov and Lindberg (1930:409–410, fig. 63), Tanaka (1931:123, col. fig. 308), Hikita (1934:10, 197–201, pl. 3, fig. 4, and pl. 11), and Okada, Uchida, and Matsubara (1935:243, col. pl. 143, figs. 1–2), and Okada and Ikeda (1938:120–121, 139, fig. 16).[1] We present figures of *Karcius bicoloratus* and *Platichthys stellatus* (Pls. I–II) from the region of Kinkazan and Matsushima Bay, where most of the hybrids (Pls. II–IV) which we have studied were taken.

[1] In this connection it may be pointed out that Jordan and Starks (1906:218–219, fig. 19), in their review of the Japanese flounders, copied Jordan and Evermann's (1898:2651–2652; 1900:3311, pl. 381) description and figure of *Platichthys stellatus*. The same figure, based on an Alaskan specimen, was recopied by Jordan, Tanaka, and Snyder (1913:330, fig. 278) and by Tanaka (1936:263, 1 fig.). The first description, still one of the best, of an Asiatic specimen of *Platichthys stellatus* was that of Steindachner (1870a:421–422).

Characters of the Hybrids

The *Kareius* × *Platichthys* hybrids were recognized as such by the circumstance that they resemble both genera in all respects in which *Kareius* and *Platichthys* are alike, and are intermediate in all characters by which the presumed parental genera differ. Some of the features (see Pl. II) were very apparent in the field, but others became obvious only after counts and measurements had been made and analyzed in the museum. Still other trenchantly intermediate characteristics were not discovered until the specimens were subjected to closer scrutiny, and until internal characters were dissected. Each new character which has been studied has added confirmation to the view that we are dealing with interspecific hybrids — until, in our minds, the last vestige of doubt as to the correctness of this interpretation has been dispelled.

Before contrasting the cross-bred flounders with the parental species we wish to point out that the hybrids agree with both forms in all respects in which they correspond with one another. Referring to the analytical criteria given by Norman (1934 : 282–286), we note that the following features (in addition to all characters, so far as they are apparent, assigned by him to the family Pleuronectidae) are all shared by the hybrids with *Kareius bicoloratus* and *Platichthys stellatus:*

> Pelvic fins . . . short-based, symmetrical, supported by the pelvic bones behind . . . the cleithra; pectoral radials present . . . . Origin of dorsal fin above the eyes, behind nasal organ of blind side; praecaudal parapophyses separate, divergent; hypocoracoid narrowed forward below . . . . Lateral line well developed on both sides of body; olfactory laminae . . . parallel, without rachis . . . . Mouth smaller, maxillary of ocular side less than ½ head . . . . Teeth larger, obtuse . . . uniserial.

The characters of the pyloric caeca, the lower pharyngeal arch, the squamation, and the head tuberculation, introduced by Norman in his key to the pleuronectine genera, are all different in *Kareius* and *Platichthys*, and hence are dealt with below.

The hybrids also agree with *Kareius* and *Platichthys* in other characters, such as those utilized in the key by Jordan and Goss (1889 : 234), which was copied by Jordan and Evermann (1898 : 2607–2608) and by Jordan and Starks (1906 : 165–166). Thus the vertebrae and the dorsal and anal rays are in moderate number [2]

[2] Incidentally, the numbers given for *Platichthys* by Jordan and his associates are lower than the stated limits for the subfamily to which the genus was referred.

(pp. 291 294), the lateral line lacks the anterior arch and the accessory dorsal branch, and the body (except in the young) is devoid of any regular or normal squamation. In correlation with the lack of an ordinary investment of scales the skin is very leathery.

We conclude that the hybrids share with *Kareius* and *Platichthys* all known characters that are common to these genera. In all the numerous features by which *Kareius bicoloratus* and *Platichthys stellatus* have been found to differ the hybrids are intermediate.

SIZE

It is probable that the hybrids are of intermediate size (see measurements in list of hybrids). They are indicated in Table I as averaging larger than either parental species, but they are no doubt smaller in the run than *Platichthys*, which is generally regarded as one of the largest of the flounders. All hybrid specimens seen in the field were preserved, despite their number and rather large size, but the specimens of *Platichthys stellatus* were selected. Throughout its range that species is often as large as or larger than the largest hybrids. When the hybrids were recognized all available specimens of *Kareius* were preserved. Hence their smaller average size, as compared with the hybrids, is probably significant. In his monograph on Chinese flounders Wu (1932 : 118) gave 325 mm. as the maximum total length for *Kareius bicoloratus*.

COLOR

Well-preserved material from the vicinity of Kinkazan and Matsushima Bay (Pl. II) indicates that the hybrids are not so pale as those of *Kareius* nor so dark as those of *Platichthys*. The senior writer's field notes on the fresh colors of the hybrids are as follows:

> They vary from the pale dirty yellowish amber of *Kareius* to the olive-slaty or purplish slaty of *Platichthys*.[3] The fins often have more yellow or orange than in *Kareius;* as much as in some specimens of *Platichthys* though not so much as in the examples of that genus with the brightest fins. The fin markings are intermediate in that they are smaller and less black than in *Platichthys stellatus*, but some hybrids approach that species in this color feature.

[3] Incidentally, it should be mentioned that the colored figures of the hybrids and the parental species which have appeared in the Japanese literature (references above) are not true enough in color to indicate the intermediacy of the hybrids in this respect.

The markings on the vertical fins provide the most striking first-glance distinction between *Kareius*, the hybrids, and *Platichthys*, and this character gradient is perhaps accentuated in preserved specimens (Pl. II). The fins of the young of *Kareius* have faint mottlings of light and dark, which almost wholly disappear with age. In *Platichthys* the fins are crossed by almost jet-black bands, which parallel the rays, occur on both sides of the fins, and often extend across the dorsal and anal bases onto the otherwise white blind side of the body; the bands on the caudal fin are similar, but usually do not reach the base of the fin. In the hybrids these markings are smaller and less barlike, and often appear rather as mottlings, which are dusky instead of black. The general pattern, however, is the same, as is the number of markings: four to ten on the dorsal fin; four to seven on the anal; only a few on the caudal.

TUBERCLES ON THE EYED SIDE

In the next most obvious external difference between *Kareius* and *Platichthys*, namely, the tuberculation of the body, the hybrids likewise clearly exhibit their origin. This is true for both surfaces of the body

Tubercles on the Eyed Side of Kareius

On the ocular side the tuberculation of *Kareius* and *Platichthys* is enormously different, except in the weakly scaled young. In *Kareius* the body in the half-grown and the adult is smooth and scaleless, save for certain rows of tubercles:[4]

1. The most conspicuous of the rough dermal ossifications form a dorsolateral row, along the line where the neural spines and interneural bones meet. This row (irregular or partly doubled or even trebled in some specimens) is best developed over the trunk and varies greatly in thickness and length. Its component elements occasionally appear in part as rounded stellate tubercles, but tend to form large rough, bony warts having an outline reminiscent of rhombic ganoid scales. A nearly solid elongate mass is often produced. This row is rarely lacking in the half-grown fish or the adult.

[4] The gross anatomy and arrangement of the spinulose osseous plates in the adults of *Kareius bicoloratus* have been described by various authors (quoted above, in most detail by Wu (1932: 10–13, figs. 1–3), who also treated the histology of these hypertrophied scales. Jordan and Hubbs (1925: 300) described the ontogeny of the aberrant squamation in *Kareius*.

2. In the ventrolateral row of tubercles, extending along the contact between the hemal spines and the interhemals, the elements are more commonly large rounded spiny tubercles; but in some fish these tend to fuse or enlarge to resemble the parts of the dorsolateral row. Not infrequently the ventrolateral scutes are very few, rudimentary, or even entirely absent. The row may be irregular, doubled, or even trebled.

3. A series of elongate bony scutes (rudimentary in some, large and wartlike in others) is frequently laid down along the narrow dermal groove which lies just above and runs parallel with the lateral line. These are often entirely lacking, even in large adults.

4. Somewhat less frequently similar ossifications occur in the corresponding groove just ventral to the lateral line. These scutes of rows 3 and 4 are not to be confused with the more or less enlarged stellate tubercles which in *Platichthys* form one or more rows on either side of and parallel to the lateral line, for those tubercles lie outside the rudimentary grooves accompanying the lateral line.

5. A more or less irregular row of stellate tubercles, occasionally swollen into bony warts, runs along the dorsolateral edge of the caudal peduncle in many specimens. These tubercles may be reduced to one or a few, and are often entirely lacking.

6. With less frequency, or to a lesser degree of development, similar tubercles form a ventrolateral series along the colored side of the caudal peduncle.

7. One or two such structures are usually evident on the base of the pectoral fin.

8. One to several are often formed just below and behind the pectoral fin. Groups 7 and 8 are developed in apparent independence, for either alone or both may be present. In one specimen a single tubercle is developed on the side of the breast.

9–11. Three groups of similar spiny tubercles comprise the squamation of the eyed side of the head. The first set lies on the interorbital ridge and in a triangular area immediately behind the ridge. The second group, along the preopercular margin, is most extensively developed dorsally. The third set covers all or part of the opercle (but not the subopercle or the interopercle). The second and third groups are more or less conjoined in some specimens. Any one of the clusters, rarely all three, may be obsolescent. Other parts

of the head, such as the body away from scale rows 1 to 8, are wholly devoid of scales.

No tubercles are ever developed in *Karcius* on the body near the base of the dorsal and anal rays, or on these rays.

Tubercles on the Eyed Side of Platichthys

In *Platichthys stellatus* (beyond the smooth, very young stages) the squamation differs strikingly from that of *Karcius bicoloratus*, as shown in the various published illustrations of the two species as well as in our two figures Pl. 1). The number and the roughness of the characteristic tubercles of *Platichthys stellatus* vary widely at each locality, and increase northward on both coasts (the race living above Kinkazan and Matsushima Bay, where the adult hybrids were obtained, is moderately rough). These structures, which replace the scales, are isolated from one another, and are stellate with small spines, like the less ossified of the plates on *Karcius*. They form one to several rows more or less parallel to the lateral line, toward which they tend to be enlarged. Toward the dorsal and anal fins the tubercles become smaller and weaker, and are commonly obsolescent in a wide strip adjacent to the row along the dorsal and anal fin bases. The scutella are often enlarged in the region behind and below the pectoral fins, near the shoulder girdle, and on the breast. Expanded and, in some fish, more or less fused platelets tend to form irregular series corresponding with rows 5 and 6 as described above for *Karcius*, along the dorsolateral and ventrolateral edges of the caudal peduncle. Rows 1 and 2, which are characteristic of *Karcius*, are not represented in *Platichthys*, even by a clumping or an enlargement of tubercles in a corresponding position. The entire length of the dorsal fin and of the anal fin in *Platichthys* is accompanied on the body by a row of spinose tubercles, which are rather regularly aligned and spaced, one opposite each interradial space (the arrangement may become irregular or even partly biserial near the front of the fins, and a few of the posteriormost tubercles are often rudimentary or obsolete). On the eyed side of the head similar stellate scale derivatives tend to be clumped in areas 9 to 11, as defined above for *Karcius*, but in addition are usually scattered over the cheek and probably always occur on the temporal region above the postocular ridge. They are commonly as well developed on the suboperele and interoperele as on the operele.

Tubercles on the Eyed Side of Hybrids

The hybrids (Pls. III-IV) vary enormously in scutellation — far more than one would expect a species to fluctuate. Some are almost wholly smooth, a few almost as rough as *Platichthys*. But in this divergence we see variously developed the tubercle patterns of both *Kareius* and *Platichthys*. The following analysis is based on twenty-five specimens, our twenty-three half-grown and adult fish and Hikita's two adults (as represented by his exquisitely detailed figures). We take up first the nine rows or areas of scutes in *Kareius*, as defined and numbered above, then follow with scale derivatives that are developed in *Platichthys* but not in *Kareius*.

1. *Dorsolateral series.* — This diagnostic feature of *Kareius* is more or less evident in twenty-four of the twenty-five larger hybrids, though it is always made up of large stellate tubercles rather than bony warts. It would seem that the tendency to form tubercles is derived more from *Platichthys*, but that the location of the series is a *Kareius* character. In nine examples the scutella of this more or less irregular series are the only ones developed between the basidorsal tubercles and the lateral line. Of these nine, one (Pl. III, Fig. 1) has only one tubercle in the series. The eight others (Pl. III, Fig. 2) have the series ranging from one third to the full body length. Five specimens comprise an intermediate category, for in them the only other tubercles between the dorsal base series and the lateral line are: (*a*) three near the lateral line anteriorly; (*b*) twelve following the course of the lateral line anteriorly and medially; (*c*) a group between series 1 and the lateral line posteriorly; (*d*) a cluster of eight between series 1 and the lateral line anteriorly; and (*e*) a group of six above the lateral line near the middle of the standard length and six others between series 1 and the lateral line posteriorly. In ten hybrids the dorsal half of the body is more or less covered with scattered platelets from near the lateral line out to an irregular longitudinal clustering that evidently represents a positional effect of series 1 of *Kareius*. In four of these ten there are additional tubercles, in varying number, between the anterior part of this clustering and the dorsal fin. One of the most heavily tuberculate examples is pictured as Plate IV. The only hybrid exhibiting no trace of the dorsolateral series is very close to *Plat-*

ichthys in squamation and all other characters, and may well be a backcross.

2. *Ventrolateral series.* — The squamation below the lateral line of the hybrids is almost a mirror image of that above the lateral line, except that the tubercles are usually fewer. The specimen with only one scutellum in series 1 (Pl. III, Fig. 1) has none over the main part of the body below the lateral line. Others in the first category of nine have as few as three spiny scales in series 2, and one of the five in the intermediate category has only one in this series. Otherwise the agreement in the dorsal and ventral tubercle pattern is close. The one specimen (a possible backcross) with no trace of series 1 likewise exhibits no evidence of series 2.

3–4. *Lateral-line series.* — Traces of these series, diagnostic of *Karcius* though often undeveloped in that genus, were detected in ten of the twenty-five larger hybrids. The individual scutes remain subcircular and small, without the elongation and warty enlargement typically seen in *Karcius*. The degree of development is various: two have only one below (that is, in series 4), three have several above (series 3), one has one above and one below, one has two above and two below, one has two above and three below, one has eight above and two below, and one has many above and below. In the hybrids the groove in which these plates develop in *Karcius* is usually indistinct, never well developed, often imperceptible. It is barely or not at all evident in *Platichthys*.

5–6. *Dorsolateral and ventrolateral rows on the caudal peduncle (extending somewhat farther forward in some specimens).* — It is consistent with the hybrid interpretation that twenty-four of the twenty-five postjuvenile specimens have several to many hard tubercles in these two series, which are commonly developed in *Karcius* and typically evident too in *Platichthys*. The one variant in this respect is the possible backcross with *Platichthys* mentioned above; it has small weak tubercles in the dorsolateral row (5).

7. *Pectoral base.* — This area, which usually bears one or two tubercles in *Karcius* and a number of generally large ones in *Platichthys*, is naked in the two least-scaled hybrids, but bears from one to many scutes in all other specimens of our series. Hikita's figures show no pectoral-base scutes in one specimen, and only one in the other.

8. *Area just below and behind the pectoral base.* — As would be

expected, from one to many stellate tubercles appear in this region, in rough proportion to the total number of plates.

9–11. *Head tubercles.* — In some of the hybrids the head scales tend to be restricted to the three regions to which they are confined in *Kareius,* but in all except one a few to many occur also on the temporal region (at least just above the postocular ridge) and on the cheeks, subopercle, and interopercle. In some the scutes are thickly and almost evenly scattered over the head, as in the most heavily armored specimens of *Platichthys.* Variable intermediacy is again the diagnosis.

The special scale features of *Platichthys* are also more or less evident in the hybrids. As indicated above and as shown on Plates III–IV, the body scutes vary tremendously in number, and are sometimes about as well developed as in *Platichthys.* In fish with many scales, and in some specimens with only a few, the tubercles near the mid-line tend (as in *Platichthys*) to form two series, one above and one below, but both definitely separated from, the lateral line. The breast, which bears only one scute in a single specimen of *Kareius* examined, but is covered with enlarged scutes in *Platichthys,* is provided in all the hybrids with several to many large tubercles. The region just behind the shoulder girdle, and intervening between the breast and the pectoral base (always naked in *Kareius,* but well armed in *Platichthys*), is scaleless in four hybrids and bears one to many large stellate tubercles in the twenty-one other specimens.

In general, the body scutes, other than those of the lateral-line series (3–4), are either well developed or absent in the hybrids, as though a threshold of development were required for their realization. This is usually evident, too, for the stellate tubercles along the dorsal and anal bases. These are totally lacking in *Kareius bicoloratus,* but are developed nearly to completeness in *Platichthys stellatus.* Instead of all or nearly all being partially formed in the hybrids, a variable number are well developed, typically without a trace of rudiments, so that each series ends abruptly posteriorly (this is occasionally not true on the eyed side, and is often untrue on the opposite side). The intermediacy seems to be primarily one of numbers — of presence or absence in varying proportion. The situation is different in the *Platichthys flesus* × *Pleuronectes platessa* cross of Europe, in which the hybrids have scales along the

fin bases intermediate between the very strongly spined scales of these rows in the *Platichthys* and the smooth scales of *Pleuronectes* (Duncker, 1895 : 15–29, figs. 6–14; Kändler, 1935 : 12, figs. 1–2; and other authors). The dorsal series in the Japanese hybrids averages longer than the ventral one, and both are usually centered near the vertical where the body depth is greatest.

In all four series of scutes along the dorsal and anal fin bases the number of elements varies beyond any reasonable expectation for a species (Table II). When the scutes are numerous they are generally more irregularly arranged than in *Platichthys*. They are often more isolated from one another and more removed from the fin base, especially on the anterior part of the series, and tend to form a double row in some specimens (in which case some small scutes may encroach on the fin base). As a result of this irregularity, the scutes of the fin-base row and of the body may more or less grade into one another, and the counts, particularly when high, are not very precise. There is evident, too, a tendency toward a cumulative increase in the count when the fin-base row is more or less doubled anteriorly. This is especially true of the basidorsal series and helps to explain the overlap between the counts for the hybrids and *Platichthys*. The number of stellate tubercles along the base of the dorsal and anal fins, on the eyed side, is almost exactly intermediate between the numbers developed in the parental species; in round numbers the average values for *Kareius*, hybrids, and *Platichthys* are 0, 30, and 57 for the basidorsal series and 0, 22, and 40 for the basianal row (Table II). The lesser development of the plates on the blind side is discussed below. The high positive correlation in the number of tubercles of the different series along the fin bases and the tendency of those with the high counts to approach *Platichthys stellatus* in color and still other features strongly suggest backcrossing between the hybrids and that species.

Small spiny tubercles appear on the longer dorsal and anal rays of two hybrids, 35 and 38 cm. in standard length, and a single one is developed on a dorsal ray in a 21-cm. example. No such scales could be found in even the largest examples of *Kareius*, and, oddly, none appear on any of the *Platichthys* specimens from the same region (Kinkazan and Matsushima Bay). Probably larger adults in northeastern Honshyû will also be found to develop scutes along the fin rays. It will be remembered, too, that this race of *P. stellatus*

TABLE II

NUMBER OF STELLATE TUBERCLES ALONG BASE OF DORSAL AND ANAL FINS IN *KAREIUS BICOLORATUS*, HYBRIDS, AND *PLATICHTHYS STELLATUS*

The counts were made only on half-grown and adult specimens from Japan: 62 of *Kareius bicoloratus*, 25 of hybrids, and 34 of *Platichthys stellatus*.

	Along dorsal base		Along anal base		Total
	Eyed side	Blind side	Eyed side	Blind side	
Number of tubercles in individual hybrids	10	0	8	0	18
	7	0	11	0	18
	11	..	11	..	..*
	11	0	14	0	25
	22	0	12	0	34
	19	0	16	0	35
	19	0	17	0	36
	19	9	17	4	49
	29	3	18	5	55
	28	3	26	4	61
	29	..	19	..	..*
	30	5	22	5	62
	26	5	26	6	63
	34	2	24	3	63
	39	0	24	0	63
	28	8	23	10	69
	26	12	24	8	70
	36	18	16	15	85
	48	8	30	2	88
	31	25	25	12	93
	47	12	29	11	99
	54	24	30	13	121
	54	26	27	17	124
	55	16	40	14	125
	50	30	29	20	129
Limits of variation					
Kareius bicoloratus	0–0	0–0	0–0	0–0	0–0
HYBRIDS	7–55	0–30	8–40	0–20	18–129
Platichthys stellatus	52–65	43–65	33–45	30–46	170–212
Averages					
Kareius bicoloratus	0.00	0.00	0.00	0.00	0.00
HYBRIDS	30.48	8.96	21.52	6.48	68.91
Platichthys stellatus	57.40	52.39	39.70	38.67	188.16

* Data taken from Hikita (1934: pl. 2)

is only moderately rough. In an example from Muroran, typical of the more rugose Hokkaido race, some scales of this sort line a few of the dorsal rays, and such scales are well developed on both dorsal and anal fins of specimens from southeastern and southwestern Alaska — both representing roughly tuberculate races. Apparently these scales are always confined to the eyed side.

TUBERCLES ON THE BLIND SIDE

The complete intermediacy of the hybrids (as individuals when all characters are considered and as a group when any one feature is taken into account) is particularly well shown by the scutellation of the uncolored surface of the body and head. The mode of inheritance of species characters is also illustrated very interestingly. Consequently this matter is subjected to a rather extensive analysis (Table III).

In the development of the dorsolateral and ventrolateral rows (1 and 2) of tubercles on the blind side of some specimens, the hybrids, in the light of the data, do not seem to be intermediate. Traces of the stronger, dorsolateral, row (1), diagnostically developed on the ocular surface of *Kareius*, appear on the blind side in a few specimens of this genus, but no trace was found of the ventrolateral row (2) on the uncolored surface of any. Nor does any trace of these rows appear on either side of *Platichthys*. Most of the hybrids have, on the blind side as well as on the ocular surface, at least a trace of the dorsolateral scutes, and six of the twenty-three examined have the ventrolateral row represented on the uncolored side. What appears to have happened is that the hybrids have inherited from *Platichthys* a tendency to form tubercles on the lower surface, and from *Kareius* the pattern of developing scutes in particular areas. They may be said to be genotypically but not phenotypically intermediate. Of course, we have in mind that the flounders remain potentially symmetrical throughout life. The bringing out on the blind side of the hybrids of the scutellar characters normal to the eyed surface of one parental species reminds us of the well-known capacity of flounders to develop pigment on the normally white side, when the lower surface is subjected to illumination (Cunningham, 1891; Osborn, 1940).

The slight development of the lateral-line tubercles of row 3 and the lack of row 4 on the blind side of the hybrids reflect the circum-

stance that these scutes, though diagnostic of *Kareius*, are often wanting or rudimentary on the eyed side. It is in general true in species hybrids that characters which are undeveloped in one parental form and rudimentary in the other (like the minute barbel of many American cyprinids) tend to be lacking in the hybrids.

Rows and groups (5–11) of tubercles which are developed on the blind side in both parental genera, though to a different degree, are also well expressed in the hybrids. The general squamation of the uncolored surface of the body and of the caudal peduncle, lacking in *Kareius* but developed in *Platichthys*, is either absent or present in the hybrids, in about equal ratio. However, in the usually coarse tuberculation on the blind side of the pectoral base and the region just below and behind this fin base, and of the breast and the strip just behind the shoulder girdle, the hybrids resemble *Platichthys* more closely than they do *Kareius*.

The most striking divergence of the hybrids from a position of exact intermediacy lies in the number of tubercles developed along the dorsal and anal fin bases (Table II and Fig. 3), on the blind side of the body. On the eyed side the number of basidorsal and of basianal tubercles is almost exactly intermediate between the zero development in *Kareius* and the almost complete development (one for each fin ray) in *Platichthys*. On the uncolored side of the hybrids, however, these tuberculations are often lacking, and on the average are only one sixth as numerous as in *Platichthys*. The greater approach to *Kareius* may be explained as due to the additive effect of two genetic factors: (1) the general tendency among flatfishes for such structures as tubercles to be less well developed or lacking on the blind side and (2) the gene or genes responsible for the total lack of these tubercles in *Kareius*.

NUMBER OF VERTEBRAE

Since the dorsal and anal rays and the lateral-line pores of *Kareius bicoloratus* outnumber those of *Platichthys stellatus* (Table IV) and since the number of fin rays and vertebrae is positively correlated in flounders (Kändler, 1935 : 13–14, 19; Townsend, 1937 : 98–102, fig. 1), as in most other fishes, we looked for a difference between these species in the number of vertebrae. That there is an average difference in the expected direction and that the hybrids are again intermediate seems to follow from the available data (see p. 291).

TABLE III

DEVELOPMENT OF TUBERCLES ON THE BLIND SIDE OF SPECIES AND HYBRIDS OF FLOUNDERS FROM JAPAN

The counts were made on 62 specimens of *Kareius* longer than 100 mm., 23 of hybrids longer than 146 mm., and 27 of *Platichthys* longer than 170 mm.

Tubercles	*Kareius*	HYBRIDS	*Platichthys*[a]
Row 1 (dorsolateral)			
Wholly lacking	54	5	27
1 or 2, minute to medium	4	1	..
Few, rudiments[b]	..	1	..
Many, rudiments[b]	..	5	..
5, minute	1	..	..
4 or 5, small to medium	..	2	..
10 to 20, minute to small	3	..	..
10 to 30, medium	..	9	..
Row 2 (ventrolateral)			
Wholly lacking	62	17	27
1, medium	..	1	..
11–18, small to medium	..	5	..
Row 3 (just above lateral line)			
Wholly lacking	57	23	27
1–3, small and rounded	4	..	..
Series, small and elongate	1	..	..
Row 4 (just below lateral line)			
Wholly lacking	62	23	27
Row 5 (upper edge, caudal peduncle)			
Wholly lacking	56	..	..
1 or 2, minute to medium	6	1	..
Few to many, rudiments[b]	..	5	..
Few to many, medium to large[c]	..	11	27
Many, large above and small below[d]	..	6	..
Row 6 (lower edge, caudal peduncle)			
Wholly lacking	62	..	..
Few, rudiments[b]	..	2	..
Many, rudiments[b]	..	4	..
Few to many, medium to large[c, e]	..	12	27
Many, large below and small above	..	5	..

[a] The specimens of *Platichthys* used for this table were selected from those collected in northern Honshyû, since the Hokkaido race is much rougher.

[b] The rudimentary nature of these tubercles is probably due to incomplete ontogeny, for the specimens so featured are among the smallest studied.

[c] Allowance was made for apparently incomplete development in smaller fish. In some of the larger specimens, especially on the ventral edge of the peduncle, most of the tubercles are weak. All the tubercles in *Platichthys* lie on the edge of the peduncle: there is no accompanying series of smaller embedded tubercles in line with rows 1 and 2.

[d] The small tubercles, mostly or all embedded, extend forward a varying distance on the body as though comprising a disconnected posterior part of the dorsolateral and ventrolateral rows (1 and 2) of the body.

[e] Often with some smaller ones above.

TABLE III (*Continued*)

Tubercles	*Kareius*	Hybrids	*Platichthys*
Group 7 (pectoral base)			
Wholly lacking	62	6	..
1–4, small to large[f]	..	17	27
Group 8 (behind and below pectoral)[g]			
Wholly lacking	62	3	..
Rudimentary	..	..	2
1–5, medium to large	..	20	..
2–many, medium to large	..	..	25
Group 9 (opposite interorbital region)			
Wholly lacking	62	9	..
Slightly developed	..	13	2
Moderately developed	..	1	9
Well developed	..	..	16
Group 10 (preopercle)			
Wholly lacking	62	13	1
Slightly developed	..	9	9
Moderately developed	..	1	15
Well developed	..	..	2
Group 11 (opercle)			
Wholly lacking	62	14	1
Slightly developed	..	8	21
Moderately developed	..	1	5
Subopercle			
Wholly lacking	62	19	19
Slightly developed[h]	..	4	8
Interopercle			
Wholly lacking	62	19	5
Slightly developed[h]	..	3	12
Moderately developed[i]	..	1	9
Well developed	..	..	1
Temporal region			
Wholly lacking	62	16	5
Slightly developed[j]	..	7	15
Moderately developed[j]	..	..	7

[f] At least one of these tubercles is large in each specimen except in a few of the smallest ones, in which the tubercles do not appear to be fully developed.

[g] This group often grades into the one (7) on the pectoral base, into those of the sides of the body, and into those along the shoulder girdle. The distinction of these areas is arbitrary.

[h] Either a few hard tubercles or many rudiments are developed.

[i] Either a few large stellate tubercles or a few small yet hard ones.

[j] These tubercles are mostly clustered just above the postocular ridge.

TABLE III (*Concluded*)

Tubercles	*Kareius*	Hybrids	*Platichthys*
Cheeks			
Wholly lacking	62	22	13
Slightly developed	..	1	11
Moderately developed	..	..	3
Sides of body[k]			
Wholly lacking	62	11	..
Few to many rudiments; or few, large and very thin; or[l] 1, large and rough; with or without rudiments	..	12	..
Usually many[m] large rough tubercles along lateral line anteriorly, usually with rudiments or tubercles outward	..	..	27
Sides of caudal peduncle and often region just in advance thereof			
Wholly lacking	62	11	..
Few, embedded rudiments	..	10	..
Medium number, embedded rudiments	..	..	6
Many rudiments (mostly embedded)	..	2[n]	13
Few to many, rough near lateral line; many rudiments outward	..	..	7
Many, rough, over peduncle	..	..	1[o]
Breast region			
Wholly lacking	62	..	..
Medium number, rudiments	..	2	..
Few to many, large	..	21	27[p]
Just behind shoulder girdle			
Wholly lacking	62	8	..
Few, rudiments	..	1	4
1–few, large (often with rudiments too)	..	14	23

[k] This area excludes rows and groups 1–8 and the shoulder girdle, the breast, and the caudal peduncle, and the region just in advance thereof.

[l] In two specimens only.

[m] One specimen has a single large tubercle on either side of the lateral line anteriorly; another has only a few above and a medium number below; all others have many rough tubercles.

[n] One of these two specimens is the one earlier indicated as a probable back-cross; the only hybrid with no trace of rows 1 and 2.

[o] This is a common type farther northward on both sides of the Pacific.

[p] The breast is almost completely covered by large rough tubercles in some specimens, and bears rudiments as well as large scattered tubercles in others.

Number of vertebrae recorded for *Kareius bicoloratus:*

11 + 26 = 37 (Wu, 1932 : 17 — Chinese material)
11 + 27 = 38 (three counts, two from specimens [5] trawled near Kinkazan, and one from the figure by Hikita, 1934 : pl. 10, fig. 2, based on the skeleton of a fish from Hokkaido).

Number of vertebrae in hybrids:

11 + 26 = 37 (two counts, from specimens collected near Kinkazan).

Number of vertebrae in *Platichthys stellatus:*

12 + 23 = 35 (Jordan and Goss, 1889 : 227).
34 (count given by Jordan and Goss, 1889 : 296, and frequently repeated).
11 + 25 = 36 (from Hikita, 1934 : pl. 11, fig. 2, based on the skeleton of a specimen from Hokkaido).
34 to 37, with mean at 35.3 (Townsend, 1936 : 19, based on 239 specimens from Washington and Alaska).
11 + 24 = 35 and 11 + 25 = 36 (in two specimens from near Kinkazan).

The average numbers of vertebrae as determined from all the available data are:

Kareius bicoloratus: 37.75
Hybrids: 37.0
Platichthys stellatus: 35.3

OTHER COUNTS AND MEASUREMENTS

The intermediacy of the hybrids is further indicated in every large series of counts and measurements that was made (Table IV). The relative position of the arithmetic means for each count and measurement is stated and graphed in Figure 3. Each average value for *Kareius* is computed as 0, and for *Platichthys* as 100, and the mean for the hybrids is located on this percentage scale, by a value which may be known as the "hybrid index." If the index is 50 per cent, the hybrid is exactly intermediate in this character; if the index is 25 per cent, the hybrid is three times closer to the one parental species (in this case *Kareius bicoloratus*) than to the other.

A glance at Figure 3 will show that the hybrids tend to be intermediate in all characters, though the deviations of some of the indices from 50 per cent (exact intermediacy) is large. The unweighted average for the fourteen characters thus analyzed is com-

[5] One of these specimens possessed a synostosis of the vertebral column definitely approaching that figured by Wu (1932 : 53, fig. 20) for *Verasper.*

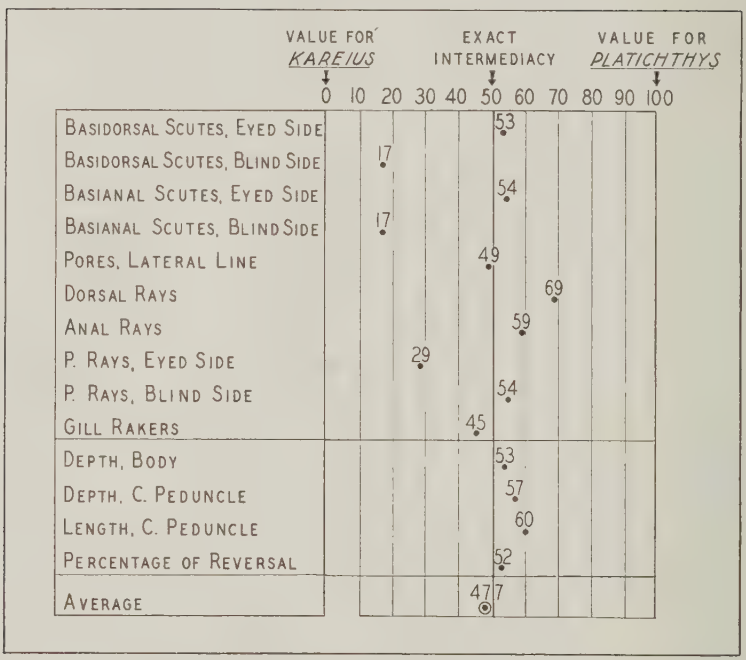

FIG. 3. Chart showing, for all statistically analyzed characters, the average values ("hybrid indices") for the *Kareius* × *Platichthys* hybrids, on a percentage scale in which the averages for *Kareius* are set at 0 and those for *Platichthys* at 100

puted as 47.7 per cent, which indicates that in the ensemble of characteristics these hybrid flounders are almost exactly intermediate between their parental species.

Since none of the frequency curves on which Table IV and Figures 3–4 were based show any obvious bimodity, it is virtually certain that the presumed hybrids are not a mixture of aberrant examples of *Kareius* and *Platichthys*. Of course, such a mixture could give a hybrid index of about 50 per cent for any given character, and for all characters, but the specimens intermediate in one respect would not be likely to be so in other features. The individual hybrid flounders here under treatment tend to be intermediate in all characters, as may be seen by inspecting Table IV and Figure 4.

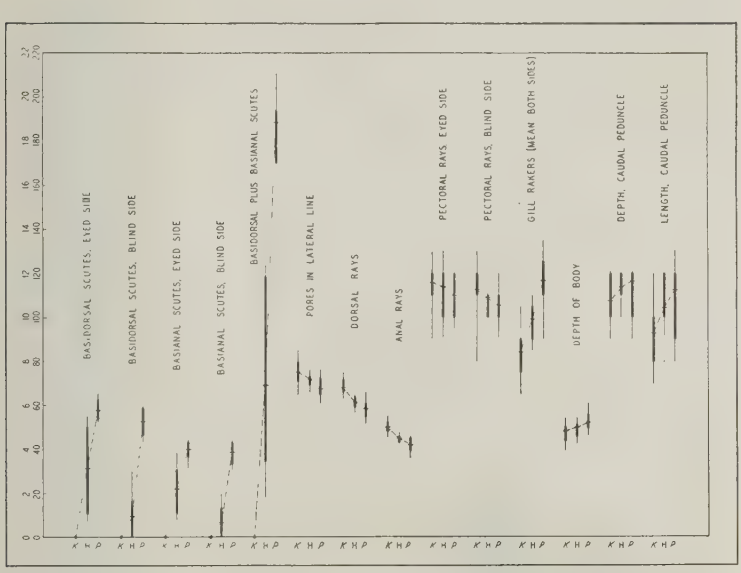

FIG. 4. Graphic portrayal of the data in Table IV, to illustrate the intermediacy of the hybrids (H) between *Kareius* (*K*) and *Platichthys* (*P*). For each of these units there are shown the total range, the usual range ("80 per cent in range" figures), and the average

Plausible reasons can be assigned for the wide deviations of certain of the hybrid characters from exact intermediacy. The greatest discrepancy, that for the number of basidorsal and basianal scutes on the blind side, has been explained (p. 287) as probably due to the additive effect of two genetic tendencies. Deviations less than 10 per cent may well be due to chance, and even greater deviations may not be significant, particularly when, as in the case of the pectoral rays, the means for the parental species are very close.

We are tempted to suggest that the relatively low number of dorsal and anal rays in the hybrids (which causes a greater resemblance to *Platichthys* than to *Kareius*) may be due to heterosis, since high metabolic rates often seem to be related to a low number of segments (Hubbs, 1926). We note, however, that the hybrids in the Baltic Sea between *Platichthys flesus* and *Pleuronectes platessa* have vertebrae and fin rays averaging higher than the mean value

between the parental species, therefore approaching the *Pleuronectes* parent more closely than *Platichthys* (Kändler, 1935). Perhaps the most logical explanation is that in Japan the hybrids are backcrossing with *Platichthys;* in the Baltic Sea, with *Pleuronectes.* This would be in line with the apparently greater abundance of *Platichthys* in the region of Japan where most of the hybrids were found, and of plaice on the flatfish grounds in Europe.

The fact that the hybrids approach *Platichthys* more closely in the proportionate measurements may have resulted from some backcrossing, but probably has little significance. The adults in these flounders have deeper bodies and deeper and longer caudal peduncles than the young, and *Platichthys* differs from *Kareius* in the same direction. The fact that the hybrids average large (since all were preserved) suffices to explain their closer resemblance to *Platichthys.*

The various deviations of the hybrid index from 50 fluctuate from the high to the low side, so that the average index, as noted above, is close to the line of exact intermediacy.

POSTOCULAR RIDGE

We have by no means come to the end of the list of characters in which the interspecific hybrids are intermediate between *Kareius bicoloratus* and *Platichthys stellatus.* The postocular ridge is another of these features. In *Kareius* this bony structure is more prominent than in *Platichthys* because it is free of scales, broader, flatter, and much more roughly sculptured with ridges and tubercles. In *Platichthys* the ridge anteriorly is typically more or less covered by strong stellate tubercles, and is relatively narrow and smooth; its posterior end, however, rises in a rather trenchant keel or winglike tubercle (flattening with age). In all these respects the postocular ridges of the hybrids range almost from the one extreme to the other, and almost all specimens very obviously exhibit intermediate or combined characteristics.

LOWER PHARYNGEALS

The lower pharyngeal arches and their dentition (Fig. 5) provided a striking confirmation of the hybrid interpretation, which we had postulated from earlier field and laboratory studies. In the northern Honshyû race of *Platichthys stellatus* the pharyngeal arches and teeth are less modified than in other members of the

Liopsetta group with which *Platichthys* is generally associated (as by Jordan and Goss, 1889:234; Jordan and Evermann, 1898: 2607–2608; Jordan and Starks, 1906:165–166; Hubbs, 1915:486; and Norman, 1934:286). The bones are united anteriorly for only about half their length, and each one is not much more than one fifth as wide as long; and the teeth are less broadened and molariform than in *Kareius*. As is well indicated by Wu (1932:116, fig. 25), the massive lower pharyngeals of *Kareius* are united for almost their entire length into a nearly solid mass, having the outline of an isosceles triangle and being provided with large molars.

Kareius Hybrid *Platichthys*

FIG. 5. Lower pharyngeal bones and teeth in Japanese specimens of *Kareius*, hybrids, and *Platichthys*

As shown in Figure 5, the arches and teeth of the hybrids are definitely intermediate in all respects. The hybrids show considerable variation in the intermediate shape of the lower pharyngeals.

ALIMENTARY CANAL

The intermediacy of the hybrids penetrates into the visceral anatomy. Contrary to a key distinction used by Norman (1934:286), the pyloric caeca differ in *Kareius bicoloratus* and in the Japanese form of *Platichthys stellatus*. In this race there occur 3 + 1 (rarely 2 + 1 or 3 + 0) caeca, in line with Norman's count (1934: 46–47, 284, fig. 28), whereas in *Kareius bicoloratus*, as in *Platichthys flesus* (Norman, 1934:377), there are 2 + 0 or 3 + 0 caeca. The three appendages at the pylorus in the Japanese type of *Platichthys* are in definite positions: (*A*) one at the outside of the pyloric bend is always well developed, finger-like; (*B*) one on the inner pyloric curve, and toward the eyed side of the body, is usually almost as well developed, occasionally rather small; (*C*) one

TABLE IV

COUNTS AND MEASUREMENTS OF *KAREIUS BICOLORATUS*, HYBRIDS, AND *PLATICHTHYS STELLATUS*

The specimens, all from Japan, have a size range shown in Table I. The data on basidorsal and basianal scutes are taken from Table II; those on percentage of reversal, from Table V. For the other characters all available specimens (listed in Table I) were utilized. The data are graphed in Figure 4.

	Kareius	HYBRIDS	*Platichthys*
COUNTS			
Basidorsal scutes, eyed side			
Extreme range	0–0	7–55	52–65
80 per cent in range*	0–0	11–50	53–62
Average	0.00	30.48	57.40
Basidorsal scutes, blind side			
Extreme range	0–0	0–30	43–65
80 per cent in range	0–0	0–16	47–59
Average	0.00	8.96	52.39
Basianal scutes, eyed side			
Extreme range	0–0	8–40	33–45
80 per cent in range	0–0	11–29	37–43
Average	0.00	21.52	39.70
Basianal scutes, blind side			
Extreme range	0–0	0–20	30–46
80 per cent in range	0–0	0–13	33–42
Average	0.00	6.48	38.67
Basidorsal plus basianal scutes			
Extreme range	0–0	18–129	170–212
80 per cent in range	0–0	34–124	170–194
Average	0.00	68.91	188.16
Pores in lateral line (from opposite upper angle of gill opening to base of caudal fin)			
Extreme range	65–85†	67–76	61–76
80 per cent in range	71–80	69–74	65–72
Average	75.51	71.56	67.48
Dorsal rays (last ray double)			
Extreme range	63–75†	57–65	52–66
80 per cent in range	66–72	59–64	55–61
Average	68.20	61.60	58.58

* The phrase "80 per cent in range" needs explanation. The figures constitute a range including at least as many specimens as the number nearest 80 per cent of the total, after the most extreme variants have been deleted.

† Similar counts are given by Wu (1932: 117, for Chinese material of *Kareius bicoloratus*.

TABLE IV (*Continued*)

	Kareius	Hybrids	*Platichthys*
Anal rays (last ray double)			
Extreme range	46–54†	43–51	36–48
80 per cent in range *	48–52	43–46	39–45
Average	49.75	45.16	42.02
Pectoral rays, eyed side			
Extreme range	9–13	9–13	9–12
80 per cent in range	11–12†	10–12	10–12
Average	11.61	11.44	11.03
Pectoral rays, blind side			
Extreme range	8–13	10–12	9–12
80 per cent in range	11–12†	10–11	10–11
Average	11.28	10.88	10.54
Gill rakers on first arch (mean of both sides)			
Extreme range	6.5–10.5	8.5–11.0	9.0–13.5
80 per cent in range	7.5–9.0	9.0–10.5	11.0–12.5
Average	8.36	9.84	11.64
Measurements in Hundredths of Standard Length			
Depth of body			
Extreme range	39–54	42–56	46–61
80 per cent in range	43–50	46–51	49–56
Average	47.00	49.44	51.63
Least depth of caudal peduncle			
Extreme range	9–13	10–12	9–13
80 per cent in range	10–12	11–12	10–12
Average	10.76	11.26	11.64
Length of caudal peducle‡			
Extreme range	7–12	8–12	8–13
80 per cent in range	8–10	10–12	9–12
Average	9.24	10.42	11.21
Percentage of Reversal			
Number counted	83 +	27	476
Percentage	0	52	100

‡ Measured along the mid-line from the caudal base to a line joining last rays of dorsal and anal fins.

on the same curve, but toward the blind side, is always smallest and may be much reduced (lacking in one of about twenty specimens examined). In *Karcius* these caeca are in corresponding position and are developed in the same size gradient, but are almost always shorter and blunter; typically the two main ones (*A* and *B*) are mere rounded protuberances at the pylorus, but *A* and sometimes both *A* and *B* are occasionally finger-like, in which case *C* may be developed as a minute to small evagination. In the Japanese *Platichthys* a fourth finger-like caecum (*D*), rarely very short, is developed (with rare exceptions) from the intestine, at some distance from the pylorus and along the line where the mesentery is attached. No corresponding structure is evident in the specimens of *Karcius* dissected. There are other differences in the alimentary canal. In the *Platichthys* there is a greater differentiation between stomach and intestine; the intestine has a thinner wall and a smaller caliber, and it is more coiled; one loop lies between the pylorus and the body wall on the blind side of the fish in the *Platichthys*, but not in *Karcius*. The general characters of the intestine as well as the caeca of *Kareius* were mentioned by Wu (1932 : 31, 33).

In the hybrids these characters of the alimentary canal, like all other known differential features, are intermediate. The caeca at the pylorus number either two or three, but at least a trace of the smallest one (*C*) is usually developed. The two main caeca are variably developed, and average smaller than in the *Platichthys* but larger than in *Karcius*. The caecum (*D*) on the intestine varies from imperceptible to moderately well developed. The intestinal characters of thickness, caliber, length, and degree of coiling are also transitional.

The North American forms of *Platichthys stellatus*, at least those from central California, southeastern Alaska and the Alaskan Peninsula, usually have pyloric caeca more like those of *Karcius bicoloratus* or the hybrids than those of the Japanese races of *Platichthys stellatus*. The number is usually 2 + 0, occasionally 3 + 0 or 3 + 1. Caeca *A* and *B* ordinarily vary from rounded elevations to short finger-like processes; caeca *C* and *D* when developed are rudimentary or very short.

SIDE BEARING EYES AND COLOR

In some ways the most interesting feature in which the hybrids are intermediate is the side which bears the eyes (Tables IV–V).

For an unknown reason, in northern Japan *Platichthys stellatus* seems always to settle onto its right side, so that the left side comes to bear the eyes and color. This constitutes a 100 per cent reversal, for the flatfishes of the family Pleuronectidae, to which *Platichthys* is clearly referable, are normally dextral. Sinistral individuals are unknown in many pleuronectids, and in most others are so rare as to be thought of as teratologically reversed in asymmetry. This subject was treated at some length, with references, by Norman (1934 : 27 29) and Gudger (1935). Both authors quoted our discovery of the uniform reversal of *Platichthys* in Japan, as well as our preliminary and inexact estimate of the degree of reversal in California and Alaska.

A large array of published and original data (Table V) indicates: (1) that *Platichthys* is particularly subject to reversal throughout its range; (2) that the percentage of reversal is a regional and racial character; and (3) that the race of southwestern Alaska seems to represent intergrades, in this respect at least, toward the regularly reversed Asiatic races. The variation in *Platichthys flesus* of Europe is great and irregular (Duncker, 1900 : 339–340; Berg, 1932 : 3 7; Norman, 1934 : 28). On the west coast of North America, from central California to southeastern Alaska, the percentage of reversal in *Platichthys stellatus* ranges irregularly from 49 to 60. About Kodiak Island and the south shore of the Aleutian Peninsula 68 per cent are reversed. For populations from the Bering Sea, Aleutian and Kamchatka regions, the data are too tenuous for safe estimates.[6] Only in northern Japan are we confident that all-sinistral races exist. Their subspecific nomenclatorial status remains to be determined.

Kareius bicoloratus seems to be regularly and perhaps invariably dextral (that is, normal for a pleuronectid). We have only eighty-three specimens on which this statement has been checked, but most of the authors quoted earlier have described *Kareius* as dextral,

[6] The counts for "Kodiak Island and the Aleutian Peninsula" in Table V include one dextral and one sinistral specimen from Akutan Island near the base of the Aleutians, and three rights and five lefts from Naknek on Bristol Bay. Scofield (1899 : 509) recorded four specimens, all sinistral, from Port Clarence, near Bering Strait, Alaska (two of these have been reëxamined), but Rendahl (1931 : 19) reported three dextral and seven sinistral specimens from the same locality and Bering Island (of the Commander group, off Kamchatka). Three examined from Kamchatka are sinistral. Several counts from Hokkaido, all sinistral, are included with those from Japan. In his study of flounders from Hokkaido, Hikita (1934) described *Platichthys* as sinistral. Most of the 476 counts

without a mention of reversed specimens, and all published figures (see p. 275) show the right side colored. Wu (1935 : 116–118) specifically stated "yeux à droite" and listed twenty-three specimens from China as having been examined.

The twenty-seven known hybrids between the dextral *Kareius bicoloratus* and the invariably reversed (sinistral) Japanese races of *Platichthys stellatus* are as nearly equally divided as is possible in respect to the side bearing eyes and color: thirteen are dextral and

TABLE V

DATA ON THE SIDE BEARING EYES AND COLOR IN CERTAIN FLOUNDERS

Based on the counts published by Lockington (1879 : 93), Scofield (1899 : 509), and Townsend (1937 : 94–97), and on original data.

Species and locality	*Number of specimens examined*	*Percentage reversed (sinistral)*
Platichthys stellatus		
California*	509	55.2
Oregon, outer coast†	65	49.2
Columbia River mouth†	225	60.4
Washington, outer coast†	247	56.3
Puget Sound‡	8,972	51.6
Southeastern Alaska§	2,498	58.2
Kodiak Island and Alaska Peninsula‖	5,129	68.0
Japan†	476	100.0
Hybrids, *Kareius* × *Platichthys*†	27	52.0
Kareius bicoloratus†	83 +	0.0

* Counts original, plus 284 from Lockington (1879 : 93) as quoted by Townsend (1937 : 96).

† Counts all original.

‡ Counts mostly furnished by the late E. Victor Smith, supplemented by the figures of Townsend (1937 : 97) and by a few original counts.

§ Counts original, mostly furnished through the kindness of Earl E. Ohmer.

‖ Data mostly from Townsend (1937 : 97), supplemented by numerous counts kindly made for us by Allan C. DeLacy, and by a few other original determinations.

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given for northern Japan were based on specimens from Matsushima Bay and off Kinkazan (where most of the hybrids were secured), but a considerable number of the determinations were made on specimens from various points throughout the known range of the species in northern Japan (p. 270 and Figs. 1–2). All published figures (see p. 275) of Asiatic specimens show the left side colored. A dextral individual of *Platichthys* was mentioned in a report of the Chosen Fisheries Experiment Station, but when reexamined by the junior author, this specimen proved to be a hybrid.

fourteen are sinistral. This is clear confirmation for the assumption, based on geographical variation, that reversal of sides is an hereditary phenomenon, perhaps involving, as does the direction of coiling in snails, some simple Mendelian segregation. The interesting point in connection with the present discussion is that the hybrids are more or less precisely intermediate between the parental species in this developmental character, which seems to have, as its determining source, some fundamental peculiarity of the nervous system in the postlarvae.

Summary

Numerous natural hybrids between species and even genera of fishes are known. These are mostly from fresh water, but occur also in the sea. In line with ecological expectation certain flatfishes (Heterosomata) are particularly wont to hybridize. In the Bothidae and Pleuronectidae there are recognized five interspecific hybrids in Europe and one in Western North America. All of these combinations are regarded by us as intergeneric.

A new interspecific flatfish hybrid, *Kareius bicoloratus* × *Platichthys stellatus*, is recognized, from Japanese waters. Like other natural hybrids in this and other families of fishes, it is intermediate in all characters and highly variable in some respects. Its rare and sporadic occurrence also suggests its interpretation as a hybrid, and the available information on the geographical distribution, habitat selection, and breeding season of the presumed parental species in Japan is quite in harmony with this view. It is suspected that the hybrids may be partially fertile. *Kareius* is regarded as generically distinct from *Platichthys*, though closely related.

The hybrids agree with *Kareius* and *Platichthys* in all features which these genera have in common, and are more or less precisely intermediate in all characters in which the genera disagree. The features in which the hybrids are variably intermediate pervade the whole organism, and include: size; general body color, and the markings on the fins; the complex arrangement, the number, and the degree of development of the modified squamation (bony plates, stellate tubercles, and rudimentary scales), on both sides of the body, head, and fin bases; the numbers of vertebrae, of lateral line pores, of dorsal, anal, and pectoral rays, and of gill rakers; the depth of the body, and the depth and length of the caudal peduncle;

also such internal differences as the shape and strength of the pharyngeal arches and teeth, the number of pyloric caeca, and the diameter and degree of coiling of the intestine; also the percentage of reversal (that is, of sinistral individuals). Like nearly all pleuronectids, *Kareius* is dextral (with eyes and color on the right side), but *Platichthys* in Japan is invariably reversed. Of twenty-seven hybrids, thirteen are dextral and fourteen are sinistral.

Not considering ordinal and family characters, which are of course held in common, we find at least twenty-one features, regarded as of subfamily or generic significance, in which the hybrids agree with both parental genera. In sixteen of the respects in which *Kareius* and *Platichthys* differ the hybrids are intermediate but closely similar to both genera. In no fewer than seventy comparisons the two parental genera are more or less trenchantly different, and the crossbred fish are intermediate. In two of these comparisons the hybrids seem unlike either parent, for on the blind side they often have dorsolateral and ventrolateral scale rows which do not appear on this side of the body in either *Kareius* or *Platichthys*. These rows are present, however, on the eyed surface of *Kareius*, so that in these exceptional features the hybrids may still be regarded as genotypically intermediate. In one or two respects only the hybrids resemble one parental genus exclusively in that they lack characters which are developed, but to only a rudimentary degree, in the other parent. The number of scutes along the bases of the dorsal and anal fin, on the ocular side of the body, diverge greatly from an exactly intermediate number, owing, we think, to the additive effect of two genetic tendencies — the factor responsible for the complete lack of the structures in *Kareius* and the general tendency in flatfishes for the rough scales to be more or less obsolete on the unpigmented side. In the ensemble of all statistically analyzed characters the average hybrid index is 47.7 per cent, on a scale in which 50 per cent denotes exact intermediacy.

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FIG. 1. *Kareius bicoloratus*, from a typical specimen 249 mm. in standard length, from off Kinkazan

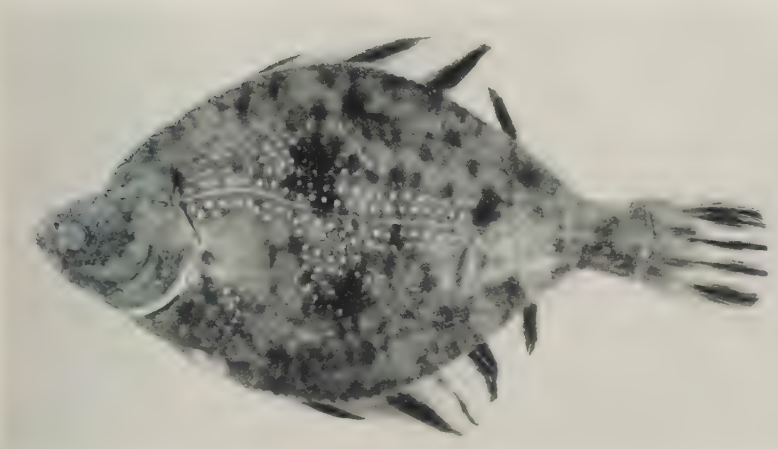
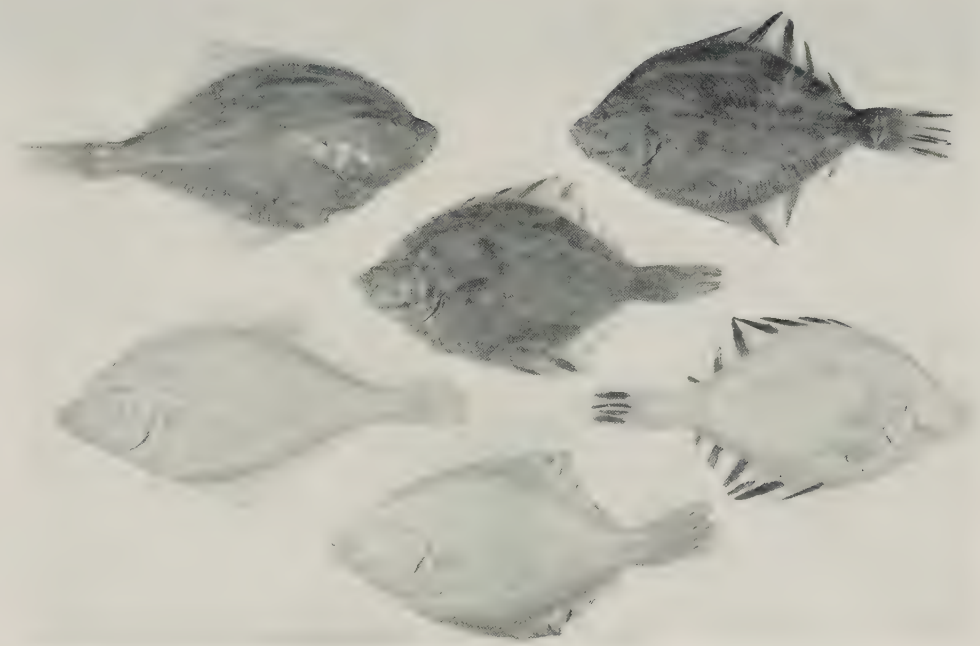


FIG. 2. *Platichthys stellatus*, from a specimen 227 mm. in standard length, typical of the race occurring off Kinkazan



Kareius bicoloratus (left), hybrids (middle two), and *Platichthys stellatus* (right), from eyed and blind sides. All adults (scale indicated by 15-cm. ruler) from the vicinity of Matsushima Bay and Kinkazan

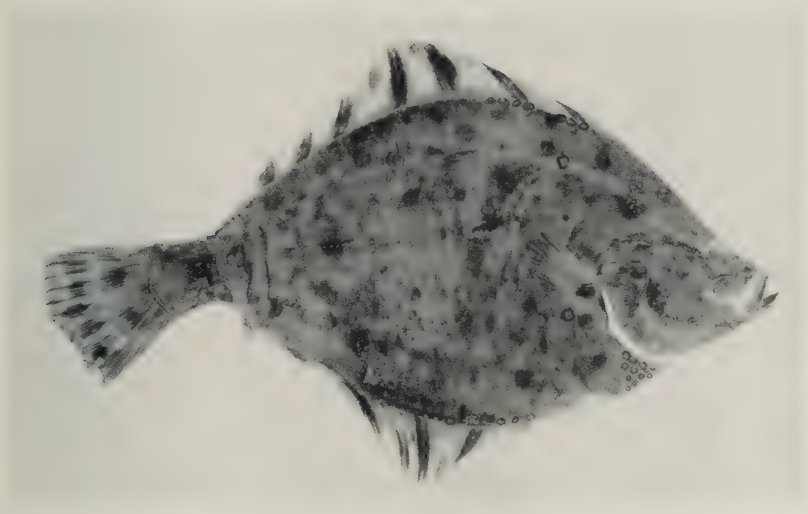


FIG. 1. The smoothest hybrid (*Kareius* × *Platichthys*), with only a single tubercle in the dorsolateral row; an adult 287 mm. in standard length, from off Kinkazan

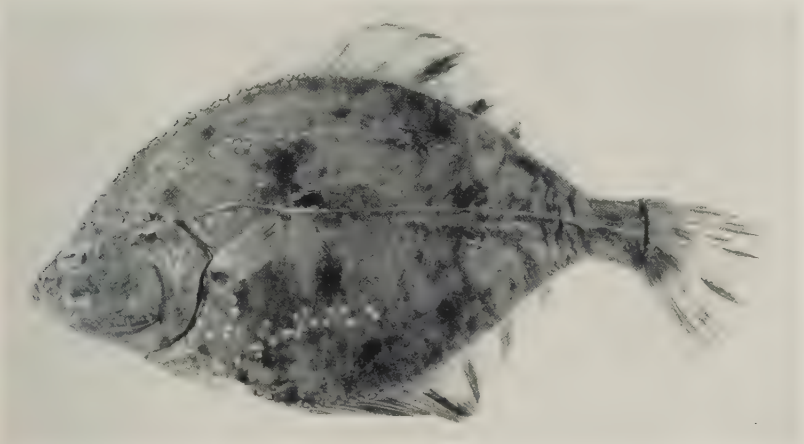
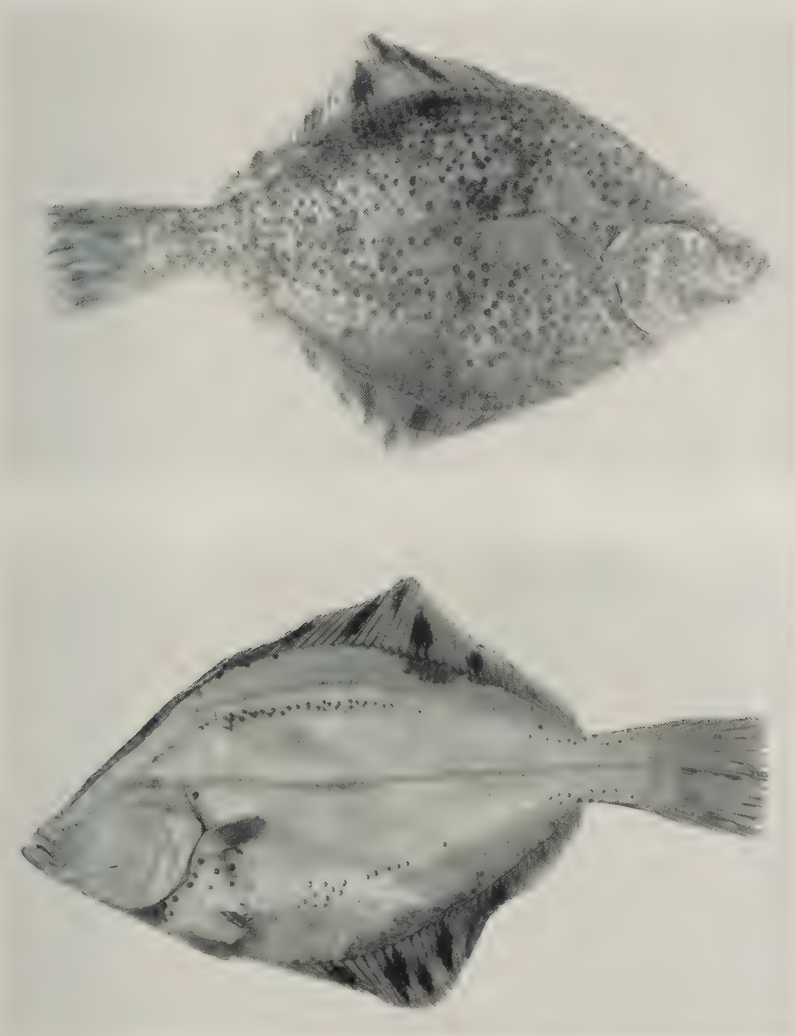


FIG. 2. A *Kareius* × *Platichthys* hybrid with a moderate number of tubercles, chiefly disposed in the dorsolateral and ventrolateral rows; an adult 361 mm. in standard length, from off Kinkazan



One of the most heavily tuberculate hybrids, an adult 320 mm. in standard length, from off Kinkazan. Both eyed and blind sides are shown. On the blind side the tubercles are mostly confined to the dorsolateral and ventrolateral rows and to the upper and lower edges of the caudal peduncle

THE AGE AND GROWTH OF THE LAKE ERIE WHITE BASS, *LEPIBEMA CHRYSOPS* (RAFINESQUE)

JOHN VAN OOSTEN

I. INTRODUCTION

ALTHOUGH the natural range of the white bass extends from New Brunswick and Minnesota southward through the St. Lawrence River, the Great Lakes region, the Ohio and Mississippi valleys to the Gulf of Mexico, the greatest concentration occurs in the Lake Erie drainage. In Lake Erie the species is restricted largely to the western end in Ohio waters, which yielded 92 per cent of the lake's commercial production (727,300 pounds, valued at $42,926) in 1938. (Only 8,400 pounds were produced in the other Great Lakes in 1938.) More than three fourths of the Lake Erie catch is taken in the spring, mostly during the spawning period of the species in May and June. About two thirds of this production is caught by trap nets.

The available annual statistics of the commercial catch (Table I) reveal no evidence of a progressive decline in the abundance of the white bass in Lake Erie, although the yearly production shows considerable periodic fluctuations. Some of the figures suggest cycles of abundance, a series of three good years being followed by four years of low yields. Had the production of the years 1927–29 been high and of 1938 low, the cycles would have been consistent and uniform during the 26-year period. The factors involved in the fluctuations of the catch are difficult to determine. The cycles suggest that some natural cause exerted the dominating influence.

Very little has been published on the age and growth of the freshwater white bass. Hile (1931) aged nine individuals collected from three Indiana lakes. Thompson (1937) aged ten specimens taken from the Rock River of Illinois. An anonymous article in *The Ohio Conservation Bulletin*, April, 1939, contains data on 617 white bass

collected in upper Sandusky Bay in Lake Erie in July and August, 1938. Of these fish 560 were aged. Eddy and Carlander (1939) summarized very briefly the ages of 69 white bass taken from several Minnesota lakes. Published statements indicate that the species may reach a maximum length of 18 inches and weight of 3 pounds.

TABLE I

Pounds of White Bass Produced Annually by the United States Commercial Fishermen of Lake Erie from 1913 to 1938

Year	Pounds	Year	Pounds	Year	Pounds
1913	511,817	1923	300,200	1934	687,700
1914	478,210	1924	181,517	1935	739,300
1915	693,537	1925	232,000	1936	663,900
3-year		1926	157,732	1937	435,100
average	561,188	1927	121,124	1938	727,300
		1928	285,179	5-year	
1916	342,780	1929	155,327	average	650,660
1917	332,778				
1918	128,972	7-year			
1919	193,347	average	204,726		
4-year					
average	249,469				
		1930	483,696		
1920	504,444	1931	418,199		
1921	840,671	1932	252,695		
1922	821,307	1933	394,400		
3-year		4-year		26-year	
average	722,141	average	387,248	average	426,278

II. MATERIALS AND METHODS

The materials used in this study were collected at several Lake Erie ports in Ohio and at Erie, Pennsylvania, in the years 1927–29 (Table III). A total of 1,869 white bass was aged, and 4,904 fish were used in the study of length-weight relationship. The Ohio specimens were taken in trap nets; the Pennsylvania fish, in pound nets. All length measurements recorded in millimeters and made with a steel tape and all weights recorded in ounces were obtained from fresh fish in the field. Determinations of sex and stage of maturity were made for only part of the fish collected. Ages are expressed by roman numerals and represent the number of annuli

found on the scales. Measurements of the projected images of the scales were taken along the anterior radius.

A study of the relationship between the length of the body and the magnified radius (scale × 40.7) of the scales used for the computation of growth was undertaken to determine whether or not there was a necessity for correcting the direct-proportion calculated lengths and, if such a correction was required, to find the method that would give the most accurate calculations of growth.

The data were grouped into five-millimeter standard length intervals and the average body length, average scale measurement, and body–scale ratio (L/Sc) determined for each interval according to age and for all ages combined. It was found that the L/Sc ratio tended to decrease (scale became relatively larger) not only as the length of the fish increased within an age group, but also as the age of the fish increased within a size group. Only the data for all ages combined are given in Table II. These showed a distinct tendency for the L/Sc ratio to decrease with an increase in the length (and age) of the fish. This progressive increase in the relative size of the scale makes necessary a correction of the direct-proportion calculated lengths to obtain accurate results.

The method for correcting the direct-proportion computed lengths was determined by plotting the averages of standard length and scale measurement of each five-millimeter length interval on coordinate paper and fitting a straight line to these data over the range represented by twelve or more individuals in each interval (range 110–244 millimeters, standard length). A line having an intercept on the "length" axis at 24 and a slope of 1.08 was found to fit closely the plotted data over the range to which it was applied (Fig. 1). The plotted values for length intervals that included fewer than twelve fish likewise deviated but little from the straight line.

The direct-proportion calculated lengths for age groups I, II, and III were corrected by the following formula:

$$L_n = \frac{L - 24}{L} l_n + 24,$$

where L_n = corrected length at end of year n,
L = standard length at capture,
l_n = average direct-proportion calculated length at end of year n,
24 = point of intercept on "length" axis.

TABLE II

Body–Scale Relationship (L/Sc) of 1,868 Lake Erie White Bass Arranged according to the Average Standard Lengths Based on Five-Millimeter Intervals, with All Age Groups Combined

Average standard length	Average scale measurement ($\times$ 40.7)	Average L/Sc ratio	Number of fish
97.2	65.9	1.47	4
102.0	78.3	1.30	3
107.0	80.5	1.33	4
112.0	81.8	1.37	13
117.5	88.6	1.33	32
122.3	92.3	1.33	46
127.0	96.0	1.32	52
132.0	100.5	1.31	59
137.0	104.7	1.31	49
142.0	110.4	1.29	61
146.9	114.4	1.29	67
152.2	118.6	1.29	76
157.0	121.1	1.30	91
161.9	127.8	1.27	142
166.6	130.2	1.28	126
171.8	134.7	1.28	159
176.7	139.6	1.27	124
181.6	143.0	1.27	83
186.4	147.6	1.26	68
192.0	154.7	1.24	66
196.9	158.7	1.24	70
202.0	166.9	1.21	88
206.6	170.9	1.21	69
212.0	174.4	1.22	74
216.6	180.0	1.20	67
222.1	182.1	1.22	49
226.6	189.4	1.20	31
231.4	192.0	1.21	23
236.6	196.9	1.20	20
241.8	201.2	1.20	12
246.2	210.0	1.17	9
251.9	207.4	1.21	9
255.8	221.0	1.16	4
261.0	216.7	1.20	3
267.0	214.5	1.24	2
273.5	227.8	1.20	2
277.0	....	....	...
282.5	254.4	1.11	2
286.2	245.8	1.16	5
291.7	266.0	1.10	3
296.0	259.7	1.14	1
Weighted average		1.26	...

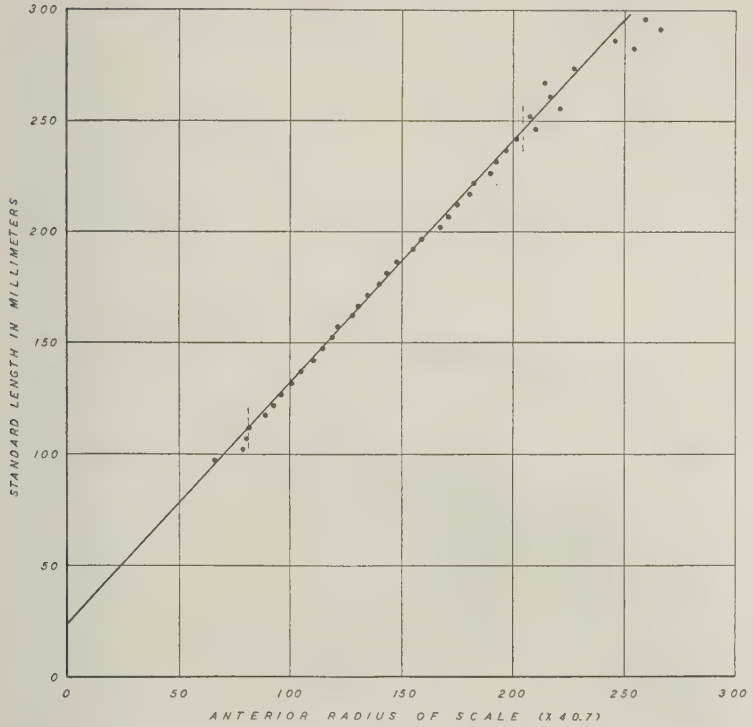


FIG. 1. Body–scale relationship (L/Sc) of the Lake Erie white bass. The two broken vertical lines indicate the length range over which the straight line was fitted. The dots are based on the averages of Table II. (See text for further explanation.)

The use of average direct-proportion calculated lengths in the formula is valid, since lengths computed by direct proportion are in effect scale lengths, and their use makes unnecessary the recalculation of individual growth histories.

The corrected calculated lengths for age groups IV, V, VI, and VII were obtained from the computation of individual growth histories, since each of these age groups contained very few individuals and the use of averages might introduce errors.

I am greatly indebted to all the members of my staff for valuable assistance rendered in the preparation of this paper.

TABLE III

AGE COMPOSITION OF THE INDIVIDUAL AND COMBINED SAMPLES OF LAKE ERIE WHITE BASS COLLECTED IN 1927, 1928, AND 1929, USED FOR THE STUDY OF AGE AND GROWTH

Date of collection	Locality	Number of fish in age group								
		0	I	II	III	IV	V	VI	VII	0–VII
Oct. 12, 1927	Sandusky, Ohio	11	366	4	..	..	..	..	..	381
Oct. 21, 1927	Vermilion, Ohio	2	7	..	..	..	..	..	..	9
Oct. 24, 1927	Sandusky, Ohio	..	19	..	..	..	..	..	..	19
Oct. 31, 1927	Sandusky, Ohio	..	30	1	..	..	..	..	..	31
Nov. 5, 1927	Sandusky, Ohio	..	17	..	..	..	..	..	..	17
Nov. 9, 1927	Sandusky, Ohio	..	27	1	..	..	..	..	..	28
Nov. 14, 1927	Sandusky, Ohio	..	51	2	..	..	..	..	..	53
Nov. 21, 1927	Sandusky, Ohio	3	14	..	..	..	..	..	..	17
1927		16	531	8	..	..	..	..	..	555
Percentage composition		2.9	95.7	1.4	..	..	..	..	..	..
Aug. 10, 1928	Huron, Ohio	..	22	95	1	..	..	..	..	118
Aug. 15, 1928	Huron, Ohio	..	13	36	..	..	..	..	..	49
Aug. 28, 1928	Huron, Ohio	..	46	115	..	..	..	..	..	161
Sept. 5, 1928	Erie, Pa.	..	35	136	..	..	..	..	2	173
Oct. 8, 1928	Erie, Pa.	..	18	80	1	1	..	1	2	103
1928		..	134	462	2	1	..	1	4	604
Percentage composition		..	22.2	76.5	0.3	0.2	..	0.2	0.6	..
July 1, 1929	Huron, Ohio	..	205	25	41	2	..	..	2	275
Aug. 14, 1929	Lorain, Ohio	..	291	..	2	..	..	..	..	293
Sept. 30, 1929	Erie, Pa.	..	36	2	9	..	..	2	1	50
Oct. 15, 1929	Erie, Pa.	..	43	10	15	..	1	1	..	70
Oct. 21, 1929	Erie, Pa.	..	16	2	4	..	..	..	..	22
1929		..	591	39	71	2	1	3	3	710
Percentage composition		..	83.2	5.5	10.0	0.3	0.1	0.4	0.4	..
1927 to 1929		16	1,256	509	73	3	1	4	7	1,869
Percentage composition		0.9	67.2	27.2	3.9	0.2	0.1	0.2	0.3	..

III. AGE COMPOSITION AND LENGTH FREQUENCIES

The age composition of the individual and combined samples of the Lake Erie white bass is given in Table III. It is apparent that the samples of any one year are comparable irrespective of the date or the place of collection. In 1927 nearly all (95.7 per cent) the fish belonged to age group I (year class 1926). Only 16 individuals out of 555 belonged to age group 0 and 8 to age group II (year class 1925). It would be of interest to know why older fish were not taken.

In 1928 no 0-group specimens were captured in the samples, either at Huron, Ohio, or Erie, Pennsylvania, and only 8 fish out of 604 were older than II. The 1926 year class as II-group fish still dominated the catch with a percentage of 76.5. Age group I (year class 1927) comprised 22.2 per cent of the samples. In 1929, however, the 1926 year class (age group III), although nearly twice as numerous as the 1927 brood, constituted only 10 per cent of the catch. The I-group fish (1928 year class) dominated the samples with a percentage of 83.2. Again the 0-group was absent, and only 9 specimens out of 710 belonged to the older age groups (IV–VII).

The data show, then, that the 1926 year class was much stronger numerically than the 1925 or the 1927 year class, and that the 1928 brood was more abundant than the 1927. Attention may again be called to the fact that the 1926 year class also dominated for several years the Lake Erie catch of yellow perch, walleyed pike, blue pike, sauger, and sheepshead (Van Oosten, 1938).

In general, it may be stated that everywhere in Lake Erie the white bass population is composed of young fish. Apparently very few individuals survive beyond their third full year. In spite of the presence of the strong 1926 year class in 1929, only 4.7 per cent of the 1,869 white bass studied were older than three years, a few reaching their eighth summer. That the paucity of old fish is due to intensive fishing cannot be asserted with certainty, although the three- and four-year-old white bass are still in the midst of their fast-growing period of life (p. 319), which fact would seem to vitiate any assumption that the III-group fish had completed their life span. Further, the majority of the fish do not begin to spawn until they reach the age of three years (p. 329).

The length frequencies of the white bass (sexes combined — no great differences existed between them) taken in the fall of the year (September 30–November 21), when the last summer's growth was virtually completed, are given in Table IV. An examination of the frequencies of age group I (the only group with sufficient number of specimens for comparison) for each year of collection separately showed that the range of the lengths of the Ohio and Pennsylvania specimens was the same, but that the eastern fish averaged about ten millimeters longer than the western. It is believed, however, that a combination of the samples of all years gives a fairly accurate picture of the length distributions of the age groups.

TABLE IV

LENGTH FREQUENCY DISTRIBUTION OF THE LAKE ERIE WHITE BASS ACCORDING TO AGE GROUPS AND TEN-MILLIMETER INTERVALS OF STANDARD LENGTH (BASED ON A COMBINATION OF SAMPLES SECURED OCT. 12–NOV. 21, 1927, OCT. 8, 1928, AND SEPT. 30–OCT. 21, 1929)

Standard length in millimeters	Equivalent mid-point, total length in inches	Age group								0-VII	
		0	I	II	III	IV	V	VI	VII	Number	Percentage
70–79	3.7	1								1	0.1
80–89	4.2	..								..	
90–99	4.7	1								1	0.1
100–109	5.2	..								..	
110–119	5.6	11	..							11	1.4
120–129	6.1	3	..							3	0.4
130–139	6.6	..	1							1	0.1
140–149	7.1	..	9	..						9	1.1
150–159	7.6	..	53	..						53	6.6
160–169	8.1	..	178	4	..					182	22.8
170–179	8.6	..	228	3	..					231	28.9
180–189	9.1	..	114	2	..					116	14.5
190–199	9.6	..	46	3	..					49	6.1
200–209	10.1	..	12	19	..	..				31	3.9
210–219	10.6	..	3	28	1	..				32	4.0
220–229	11.1	..	..	21	..	..				21	2.6
230–239	11.6	..	..	16	4	..				20	2.5
240–249	12.1	..	..	4	10	..				14	1.8
250–259	12.5	..	..	2	9	..	..	..	..	11	1.4
260–269	13.0	..	..	..	5	..	..	..	..	5	0.6
270–279	13.5	..	..	..	..	1	..	1	..	2	0.2
280–289	14.0	..	..	..	..	..	1	3	2	6	0.8
290–299	14.5	..	..	..	..	..	..	..	1	1	0.1
Total		16	644	102	29	1	1	4	3	800	

The lengths ranged from 75 to 295 millimeters, standard length, or from 3.7 to 14.5 inches, total length. The mode of the combined samples occurred at the standard length of 175 millimeters (8.6 inches, total length), and corresponded with the mode of the I-group fish. The average size of all fish was 9 inches, total length, and 87 per cent of the white bass varied between the 7.1- and 11.1-inch length intervals. Approximately 62 per cent of the individuals taken in the impounding nets were below Ohio's legal size limit of 9 inches, total length.

IV. GROWTH IN LENGTH AND WEIGHT

Only the 1929 collections provide data on the differential growth of the sexes. In 1927 all the mature white bass that were sexed were males, and sex could not be determined with certainty in the immature fish. None of the 1928 specimens was sexed. A comparison of the standard lengths, weights, and computed lengths of 263 males and 229 females of age group I collected at Huron (four fish not sexed) and Lorain, Ohio, in 1929 showed very slight differences between the sexes. At both localities the females averaged 2 millimeters longer than the males at the end of the first year of life, and the average standard lengths and weights of the females exceeded those of the males by 2 and 4 millimeters and 0.11 and 0.28 ounce.

Greater discrepancies existed between the less well represented sexes of the II- and III-group fish (24 and 41 specimens, respectively). In each group the females averaged longer and heavier. The differences ranged from 6 to 13 millimeters and from 0.9 to 1.6 ounces. However, the grand average calculated lengths of each sex of all age groups combined (285 males, 278 females) differed by only 1 and 2 millimeters in the first and second years of life and by 11 millimeters in the third. The most adequate data indicate, then, that the females are only slightly larger than the males at corresponding ages. A study of growth may, therefore, be based on the combined figures of both sexes.

An examination of the average standard lengths of the fish of each age group for each date of collection indicated that no seasonal growth occurred after the middle of October. The growth data collected in 1927 (see dates in Table III) may, therefore, be combined for all dates for each age group. The I-group fish taken in 1928 at Erie, Pennsylvania, increased their average standard length 24 millimeters from September 5 to October 8, and the II-group individuals increased it 11 millimeters. Similarly, during the period July 1 - October 21, 1929, the I-group white bass of Lake Erie apparently grew 61 millimeters, the II-group 39, and the III-group 22. To compare the actual lengths and weights of the fish captured in the three years and at different localities it is necessary that only the materials collected in late fall be employed, since the 1927 data were taken late in the season (Table V). Comparisons may also be made, however, for other seasons, provided that the dates of collection are approximately the same.

TABLE V

AVERAGE LENGTH, WEIGHT, AND COEFFICIENT OF CONDITION (K) OF THE AGE GROUPS OF LAKE ERIE WHITE BASS COLLECTED IN THE LATE FALL OF 1927, 1928, AND 1929

Age group	Locality	Year and period of collection	Number of fish	Total length (inches)	Standard length (mm.)	Average weight (ounces)	Average weight (grams)	K
0	Sandusky; Vermilion, Ohio	Oct. 12–Nov. 21, 1927	16	5.5	112	1.08	31	2.15
I	Sandusky; Vermilion, Ohio	Oct. 12–Nov. 21, 1927	531	8.4	171	4.15	118	2.31
	Erie, Pa.	Oct. 8, 1928	18	9.0	183	5.39	153	2.43
	Erie, Pa.	Oct. 15–21, 1929	59	9.1	185	5.47	155	2.41
	Grand average and total		608	8.5	173	4.31	123	2.32
II	Sandusky, Ohio	Oct. 12–Nov. 14, 1927	8	8.3	169	3.84	109	2.24
	Erie, Pa.	Oct. 8, 1928	80	10.7	217	9.30	264	2.55
	Erie, Pa.	Oct. 15–21, 1929	12	11.4	232	11.19	317	2.54
	Grand average and total		100	10.6	215	9.09	258	2.52
III	Erie, Pa.	Oct. 8, 1928	1	12.4	252	14.50	411	2.57
	Erie, Pa.	Sept. 30–Oct. 21, 1929	28	12.2	248	13.70	388	2.53
	Grand average and total		29	12.2	248	13.73	389	2.53
IV	Erie, Pa.	Oct. 8, 1928	1	13.5	273	15.25	432	2.12
V	Erie, Pa.	Oct. 15, 1929	1	14.1	285	19.25	546	2.43
VI	Erie, Pa.	Oct. 8, 1928	1	14.2	288	20.75	588	2.46
	Erie, Pa.	Sept. 30–Oct. 15, 1929	3	13.8	281	19.33	548	2.43
	Grand average and total		4	14.0	283	19.68	558	2.44
VII	Erie, Pa.	Sept. 5–Oct. 8, 1928	4	14.2	288	22.56	641	2.68
	Erie, Pa.	Sept. 30, 1929	1	14.1	285	19.50	553	2.39
	Grand average and total		5	14.2	287	21.95	623	2.62

The data of Table V indicate that the white bass of corresponding age groups averaged considerably smaller at Sandusky, Ohio, than at Erie, Pennsylvania. For example, Ohio's minimum legal size limit of 9 inches, total length, was reached in the third summer of life by the Sandusky specimens, but at the end of the second summer by the Erie fish. A comparison of the I-group fish taken in August (Table VI) shows that the specimens captured at Lorain, Ohio, in 1929 averaged smaller than those taken at Huron, Ohio, in 1928. It was also observed that age groups I and II taken at Huron in August, 1928 (Table VI), averaged larger than those collected at Erie in September, 1928 (not shown separately in Table VI). It appears, then, that no consistency existed in the discrepancies in the average lengths and weights of the fish from the two ends of Lake Erie.

It may likewise be seen from Table V that the I-group fish captured at Erie in October, 1928 and 1929, agreed extremely well with respect to length and weight, but that the II-group individuals differed widely in the two years — the 1928 specimens were the smaller. These inconsistencies in the average sizes of the fish collected in the different localities or at approximately the same time in different years suggest that no differential growth obtains among the white bass as the result of inhabiting various sections of the lake.

The observed discrepancies in the average sizes of the fish collected in different areas or years are in part the results of a differential growth of the year classes, as indicated by the data of Table VI. In this table the computed lengths and other information concerning the larger collections are arranged according to year classes. It is to be noted that each younger year class shows an improvement in computed growth at all localities. The 1925 year class is probably not well enough represented to be considered. The first year's growth increased progressively from a grand average of 90 millimeters in 1926 to 99 in 1927 to 107 in 1928. Whether this change had any connection with the unusual abundance of the 1926 year class (p. 313) is not known, but other investigators have found a relation between growth and density of population. At any rate, the small average size of the Sandusky fish is accounted for by the relatively slow rate of growth of the 1925 and 1926 year classes. A similar explanation will account for some of the other discrepancies referred to above (p. 317). It is possible, however, that the Huron

TABLE VI

STANDARD AND COMPUTED LENGTHS OF THE LAKE ERIE WHITE BASS OF THE LARGER COLLECTIONS ARRANGED ACCORDING TO YEAR CLASSES

Year class	Age group	Locality	Year and period of collection	Number of fish	Standard length (mm.)	Computed length at end of year		
						1	2	3
1925	II	Sandusky, Ohio	Oct. 12–Nov. 14, 1927	8	169	90	136	..
1926	I	Sandusky; Vermilion, Ohio	Oct. 12–Nov. 21, 1927	531	171	91	.	
	II	Huron, Ohio	Aug. 10–28, 1928	246	206	90	169	.
	II	Erie, Pa.	Sept. 5–Oct. 8, 1928	216	210	89	161	
	III	Huron, Ohio	July 1, 1929	41	226	92	164	222
	III	Erie, Pa.	Sept. 30–Oct. 21, 1929	28	248	88	162	219
	Grand average and total			1,062		90	165	221
1927	I	Huron, Ohio	Aug. 10–28, 1928	81	165	98		
	I	Erie, Pa.	Sept. 5–Oct. 8, 1928	53	167	99		
	II	Huron, Ohio	July 1, 1929	25	194	103	182	..
	II	Erie, Pa.	Sept. 30–Oct. 21, 1929	14	230	93	176	
	Grand average and total			173		99	180	..
1928	I	Huron, Ohio	July 1, 1929	205	128	116		.
	I	Lorain, Ohio	Aug. 14, 1929	291	149	102		
	I	Erie, Pa.	Sept. 30–Oct. 21, 1929	95	181	104		
	Grand average and total			591		107		.

fish actually grew somewhat faster than those of corresponding ages from Lorain and Erie.

It may also be observed from Table VI that with few exceptions the comparable calculated averages agree fairly well within a year class, irrespective of the age group, locality, or date of collection that is involved. These agreements substantiate the suggestion made above that with respect to growth the Lake Erie population of white bass is probably homogeneous. Further, in studying the computed growth of a year class the dates of collection may be ignored and the growth materials combined.

To obtain a general picture of the growth in length of the Lake Erie white bass we may combine all of our calculated-growth materials for each age group and for all age groups (Table VII and Fig. 2). The white bass exhibits a typical growth curve which rises

TABLE VII

SUMMARY OF THE AVERAGE CALCULATED LENGTHS AND INCREMENTS OF LENGTH FOR EACH YEAR OF LIFE OF THE LAKE ERIE WHITE BASS COLLECTED IN 1927, 1928, AND 1929

Age group	Number of fish	Standard length (mm.)*	Calculated length (mm.) at end of year of life						
			1	2	3	4	5	6	7
0	16	112	..	..	..	..	..	..	..
I	1,256	159	99	..	..	..	..	..	..
II	509	207	90	166	..	..	..	..	..
III	73	235	90	163	220	..	..	..	..
IV	3	250	100	174	210	241	..	..	..
V	1	285	111	200	249	266	279	..	..
VI	4	283	102	188	230	250	266	275	..
VII	7	289	103	178	230	255	268	276	283
Grand averages and total	1,869	..	96	166	221	252	268	276	283
Differences between calculated lengths (increments)			96	70	55	31	16	8	7
Equivalent total lengths in inches ...			4.7	8.2	10.9	12.4	13.2	13.6	14.0
Number of fish			1,853	597	88	15	12	11	7

* These lengths should not be used to indicate the average size of an age group since the fish were captured at various times of the year. The more valid lengths are given in Table V.

very rapidly in the first three years, then slopes gradually toward a straight line. The greatest growth occurred in the first year (96 millimeters), followed by a progressive decline that lasts through the seventh year of life.

In Table VIII are given the computed weights of the white bass that correspond with the grand average calculated lengths shown at the bottom of Table VII. The equation employed for the computation of weights is given on page 322. These calculated weights presumably provide a more accurate picture of the general growth in weight than do the actual weights shown in Table V, since they are based on all age groups combined and represent completed years of life. Both the total weights and increments of weight shown in Table VIII are plotted in Figure 3. In contrast to length, the weight

increased slowly during the first year. The curve of total weight rises rapidly, however, in the second year, then more rapidly in the next two years, after which it breaks and in the fifth year resumes approximately the slope of the second year, while in the last two years, though continuing the break, it still rises more rapidly than in the first year. The greatest increment in weight occurred in the

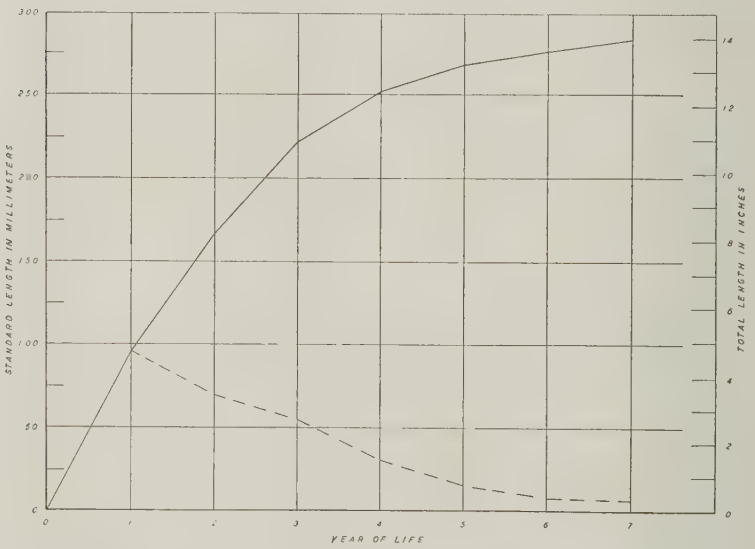


Fig. 2. Growth curves of the Lake Erie white bass. The solid line represents computed lengths; the broken line, computed increments of length. The curves are based on the grand averages of Table VII

third year, and the smallest in the first. On the basis of the increase in weight alone it would be economically sound to protect the white bass from capture until at least their fourth summer, after they have reached a total length of 11 inches (223 millimeters, standard length). Even in the fourth summer the fish added 4.8 ounces to their weight. It is of interest to record here that also on the basis of attainment of sexual maturity a size limit of 11 inches is deemed desirable (p. 329). On the Great Lakes no size limit exceeds $9\frac{1}{2}$ inches in total length.

TABLE VIII

CALCULATED WEIGHTS IN GRAMS AND OUNCES OF LAKE ERIE WHITE BASS CORRESPONDING TO THE GRAND AVERAGE CALCULATED LENGTHS OF TABLE VII, ANNUAL INCREMENTS OF WEIGHT, AND ANNUAL PERCENTAGE INCREASE IN WEIGHT

(See page 322 for the equation employed for the computation of weights.)

Item	Year of life						
	1	2	3	4	5	6	7
Calculated weight (grams)	20	108	266	401	486	533	577
Increment of weight	20	88	158	135	85	47	44
Percentage increase	..	440	146	51	21	10	8
Equivalent calculated weight in ounces	0.70	3.81	9.38	14.14	17.14	18.80	20.35

V. GROWTH COMPENSATION

To ascertain the relationship between the length of the first year and the later growth the white bass of several age groups were divided into three size classes based on the computed lengths at the end of the first year (Table IX). The average calculated length and increment of length were then determined for each size group for each year of life. It may be observed from the table that each succeeding group of larger yearlings maintained the advantage of size throughout the three or four years compared, although in general the maximum differences between the groups diminished progressively with increase in age. The increments of the second year were in close agreement and showed no decided trend in direction. The third-year increments, however, reversed the trend of the first-year figures, and the smaller yearlings showed the better growth. A compensation in growth seemed to have taken place during the third year.

VI. LENGTH–WEIGHT RELATIONSHIP AND COEFFICIENT OF CONDITION

The length–weight relationship of the white bass may be expressed by the following equation:

$$W = cL^n,$$

where W = weight in grams,

L = standard length in millimeters,

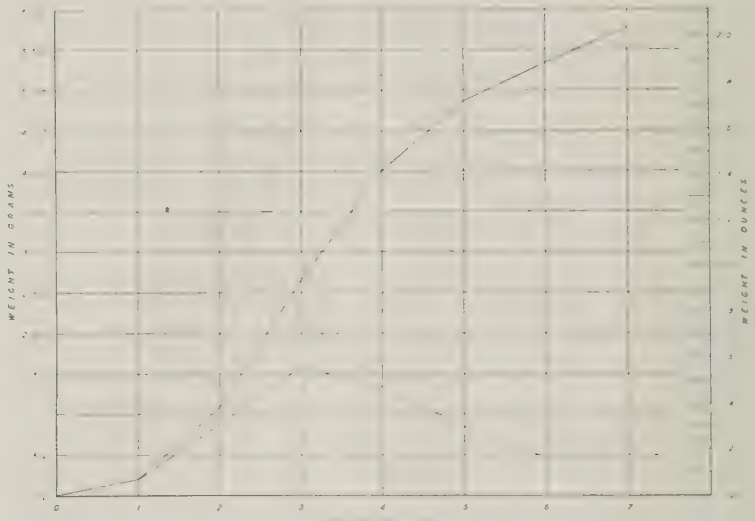


FIG. 3. Growth curves of the Lake Erie white bass. The solid line represents computed weights; the broken line, computed increments of weight. The curves are based on the averages of Table VIII

and c and n are constants, whose values are determined empirically by fitting a straight line to the logarithms of the average standard lengths and actual weights given in Table X. The equation was fitted to the average lengths and weights of fish between the limits of 103 and 261 millimeters, standard length (*A* and *B* on the curve of Figure 4). The resultant equation is: $W = 1.206 \times 10^{-5} L^{3.132}$. The equation, in logarithmic form, is as follows:

$$\log W = -4.9186623 + 3.132 \log L.$$

The curve of Figure 4 was plotted from the standard lengths and calculated weights of Table X. The dots in the figure represent the length weight relationship as based on actual measurements, which are also given in Table X. It is apparent from the figure, as well as from the differences between the actual and computed weights (column 7, Table X), that the calculated and empirical figures agree remarkably well when large enough numbers of specimens are employed. The equation may be used with confidence. The data

TABLE IX

Relationship between the First-Year Length and the Later Growth in Length of the Lake Erie White Bass

Age group, date, and locality of capture	Number of fish	Interval of calculated length, in mm., at end of first year	Calculated length at end of year of life				Calculated increment of length in year of life			
			1	2	3	4	1	2	3	4
II Aug. 28, 1928, Huron, Ohio	29	Less than 86	80	158	204*	..	80	78	46*	..
	40	86–94	90	170	212*	..	90	80	42*	..
	46	More than 94	101	178	216*	..	101	77	38*	..
	Maximum difference		21	20	12	..	..	..	..	..
II Sept. 5, 1928, Erie, Pa.	48	Less than 86	80	150	199*	..	80	70	49*	..
	49	86–94	90	162	208*	..	90	72	46*	..
	39	More than 94	100	172	213*	..	100	72	41*	..
	Maximum difference		20	22	14	..	..	..	..	..
III July 1, 1929, Huron, Ohio	11	Less than 86	80	156	213	217*	80	76	57	4*
	15	86–94	89	160	220	225*	89	71	60	5*
	15	More than 94	105	177	231	235*	105	72	54	4*
	Maximum difference		25	21	18	18	..	..	..	..

* Incomplete growing season

indicate that at the attainment of Ohio's legal length (9 inches) the white bass average 4.9 ounces in weight.

Figure 4 has been drawn so that lengths may be converted readily from standard to total and vice versa, and weights from grams to ounces and vice versa. The conversion of standard, fork, and total lengths or of lengths to equivalent weights has a practical value, since legal size limits of fish are stated in these various units of measurement in the different states. The factors that may be used to convert the various lengths are given in Table XI. A single factor is employed for each type of conversion, since no significant or consistent variation in the value was found with a change in the length of the fish.

The coefficient of condition, K, is determined by the now well-known equation $K = \frac{W \times 10^5}{L^3}$, where W = weight in grams and L = standard length in millimeters. A relatively large value of K

TABLE X

LENGTH–WEIGHT RELATIONSHIP OF LAKE ERIE WHITE BASS, BASED ON ACTUAL LENGTHS AND WEIGHTS OF 4,904 INDIVIDUALS TAKEN IN 1927, 1928, AND 1929

The average standard lengths are based on five-millimeter intervals, with sexes combined.

Average standard length in mm.	Equivalent fork length in inches	Equivalent total length in inches	Average weight in ounces	Average weight in grams	Calculated weight in grams*	Difference between actual and calculated weight in grams	*K*	Number of fish
93	4.3	4.6	0.6	18	18	0	2.19	2
97	4.5	4.8	0.7	21	20	−1	2.33	9
103	4.7	5.1	0.9	25	23	−2	2.28	13
107	4.9	5.3	1.0	28	27	−1	2.29	25
112	5.2	5.5	1.2	33	32	−1	2.32	59
117	5.4	5.8	1.3	37	36	−1	2.32	99
122	5.6	6.0	1.5	43	41	−2	2.36	135
127	5.9	6.3	1.7	48	47	−1	2.32	133
132	6.1	6.5	1.9	54	53	−1	2.33	159
137	6.3	6.8	2.1	60	59	−1	2.33	155
142	6.5	7.0	2.4	67	66	−4	2.34	148
147	6.8	7.2	2.6	73	74	1	2.29	167
152	7.0	7.5	2.8	80	82	2	2.28	198
157	7.2	7.7	3.2	89	91	2	2.31	240
162	7.5	8.0	3.5	99	100	1	2.33	300
167	7.7	8.2	3.8	107	111	4	2.31	319
172	7.9	8.5	4.2	118	121	3	2.32	359
177	8.2	8.7	4.5	128	133	5	2.31	320
182	8.4	9.0	4.9	140	145	5	2.31	299
187	8.6	9.2	5.4	152	158	6	2.33	245
192	8.8	9.5	5.9	167	171	4	2.36	168
197	9.1	9.7	6.6	187	186	−1	2.44	154
202	9.3	10.0	7.2	203	201	−2	2.47	143
207	9.5	10.2	7.7	219	217	−2	2.46	101
212	9.8	10.5	8.3	234	233	−1	2.46	121
217	10.0	10.7	8.9	252	251	−1	2.47	95
222	10.2	10.9	9.6	272	270	−2	2.49	121
227	10.5	11.2	10.3	291	289	−2	2.49	125
232	10.7	11.4	11.0	313	310	−3	2.50	100
237	10.9	11.7	11.7	332	331	−1	2.50	83
242	11.2	11.9	12.5	354	353	−1	2.50	90
247	11.4	12.2	13.2	376	377	1	2.49	81
251	11.6	12.4	14.0	396	396	0	2.50	58
256	11.8	12.6	14.9	424	421	−3	2.52	32
261	12.0	12.9	15.7	445	448	3	2.51	18
266	12.3	13.1	17.3	491	475	−16	2.61	4
273	12.6	13.5	18.0	510	515	5	2.51	4
278	12.8	13.7	18.2	517	546	29	2.41	2
282	13.0	13.9	19.5	553	570	17	2.46	1
286	13.2	14.1	20.8	589	596	7	2.52	5
292	13.5	14.4	21.1	597	636	39	2.40	5
297	13.7	14.6	19.9	565	671	106	2.15	3
302	13.9	14.9	24.2	685	707	22	2.49	2
308	14.2	15.2	25.6	726	752	26	2.49	2
310	14.3	15.3	27.5	780	767	−13	2.62	1
324	14.9	16.0	27.5	780	881	101	2.29	1

* Calculated by means of the equation, $W = 1.206 \times 10^{-5} L^{3.125}$

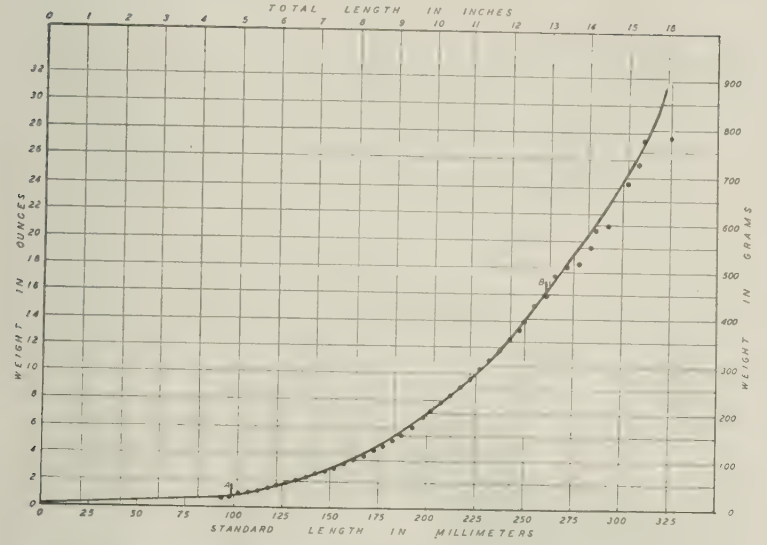


FIG. 4. Length–weight relationship of the Lake Erie white bass. The two vertical bars, *A* and *B*, indicate the length range over which the curve was fitted. The dots are based on the average standard lengths and actual weights of Table X. (See text for further explanation.)

represents a good condition of the fish. A comparison of the average *K* values of male and female white bass of corresponding age groups collected at the same locality and at the same time revealed no significant differences (0.00 to 0.08) between the sexes. The two larger samples (201 and 291 fish of age group I), collected at Huron, Ohio, on July 1, 1929, and at Lorain, Ohio, on August 14, 1929, each showed a discrepancy of only 0.03 between the sexes. The II-group fish (13 males, 11 females) captured at Huron, July 1, 1929, exhibited no difference, and the III-group specimens (9 males, 32 females) taken with the II-group differed by 0.08.

No significant variations (greatest difference = 0.06) existed between the fish (sexes combined) of age groups I, II, and III collected at Huron, Ohio, on July 1, 1929. However, the specimens of age groups I and II, taken at Erie, Pennsylvania, in the fall (Table V) showed a discrepancy of 0.13, although no significant differences existed between the II- and the III-group fish (0.02) or between the

TABLE XI

FACTORS FOR THE CONVERSION OF STANDARD, FORK, AND TOTAL LENGTHS OF LAKE ERIE WHITE BASS, BASED ON ACTUAL STANDARD AND TOTAL LENGTH MEASUREMENTS OF 1,156 FISH BETWEEN 96 AND 267 MILLIMETERS, STANDARD LENGTH, AND ON STANDARD AND FORK-LENGTH MEASUREMENTS OF 1,050 FISH BETWEEN 105 AND 211 MILLIMETERS, STANDARD LENGTH

Item *	*Conversion factor*
T. L. to S. L. (no change in units of length)	0.7978
T. L. (inches) to S. L. (millimeters)	20.2641
S. L. to T. L. (no change in units of length)	1.2534
S. L. (millimeters) to T. L. (inches)	0.0493
F. L. to S. L. (no change in units of length)	0.8548
F. L. (inches) to S. L. (millimeters)	21.7119
S. L. to F. L. (no change in units of length)	1.1699
S. L. (millimeters) to F. L. (inches)	0.0461
T. L. to F. L. (no change in units of length)	0.9334
F. L. to T. L. (no change in units of length)	1.0714

* S. L. = standard length; F. L. = fork length; T. L. = total length

I- and the II-group individuals (0.07) captured at Sandusky, Ohio, in the fall. The K (2.15) of the 0-group taken at Sandusky was relatively low.

The I- and II-group fish from Erie appear to be inconsistent. This inconsistency, however, is due not to the difference in age but to that in length (184 and 219 millimeters). Table X, in which the K values are arranged according to the length of the fish, shows that these values remain fairly constant up to a length of 192 millimeters, standard length, and then gradually increase as the fish become longer up to a length of 278 millimeters, when the values drop, although not to the level of those for the smaller fish. It appears, then, that no important changes in K are associated with an increase in the age of the fish.

An examination of the averages of K, comparable as to age group and season of collection, indicated that the Huron and Lorain specimens (age group I) differed by a value of 0.07 (2.39 and 2.32 respectively) and the Sandusky and Erie fish by values of 0.11 (age group I) and 0.31 (age group II, Table V). These discrepancies are not due to the different years of collection, since the Huron and

TABLE XII

MONTHLY AVERAGES OF THE COEFFICIENT OF CONDITION (K) OF THE LAKE ERIE WHITE BASS COLLECTED IN 1927, 1928, AND 1929, GROUPED ACCORDING TO THREE INTERVALS OF AVERAGE STANDARD LENGTH AND AGE GROUPS

The numbers of the specimens employed are given in parentheses.

Average standard length interval in mm.	Age group	July	August	September	October	November	Average
128–171	I	2.39 (205)	2.33 (372)	2.39 (35)	2.25 (122)	2.53 (109)	2.33 (1,143)
175–188	I and II	2.33 (25)	..	2.46 (36)	2.42 (77)	..	2.41 (138)
206–233	II	..	2.48 (246)	2.41 (136)	2.55 (92)	..	2.47 (474)

Lorain materials were taken in 1929, and no important variations existed in the Erie values for the years 1928 and 1929 (Table V). The white bass captured in the eastern end of the lake had higher K values than those taken in the western areas. Again, it appears that the discrepancies are associated with length rather than with localities, since the Erie fish averaged larger than those of the other ports involved.

Some idea of the extent of monthly fluctuations in the value of K may be obtained from the data of Table XII. The coefficients of age groups I and II have been combined for the sexes, localities, and years of collection. Since it was found that length was a significant factor in the variability of K, the data of Table XII have been grouped according to the average standard length of the fish of the different collections. The July individuals of the 175–188-millimeter group are 1-year fish; the other specimens belong to age group II. The October specimens of the 206–233-millimeter length interval averaged 13 millimeters longer than the group of the next largest fish, and this no doubt accounts for their high value of K (2.55). There does not appear to exist a consistent trend in K as the season advances, except that in November the coefficient of condition was high (2.53). The averages for each size class again

show the correlation between the value of K and the length of the fish. The grand average of K based on 1,755 specimens is 2.37.

VII. SEX RATIO

As stated on page 315, only the 1929 materials provide adequate information on the relationships between the sexes. The data on sex ratios, given in Table XIII, show an increase in the percentage of females with age, although the older fish are not well represented.

TABLE XIII

SEX RATIOS OF THE LAKE ERIE WHITE BASS COLLECTED IN 1929

Age group	Locality	Date	Total number of fish	Number of males	Number of females	Percentage of males	Percentage of females
I	Huron, Ohio	July 1	201	117	84	58	42
	Lorain, Ohio	August 14	291	146	145	50	50
	Total		492	263	229	54	46
II	Huron, Ohio	July 1	24	13	11	54	46
III	Huron, Ohio	July 1	41	9	32	22	78
IV	Huron, Ohio	July 1	2	0	2	0	100
VII	Huron, Ohio	July 1	2	0	2	0	100
I–VII	..	..	561	285	276	51	49

Among the I-group fish collected at Huron the males comprised 58 per cent of the sample, which percentage was reduced to 54 in the II-group and to 22 in the III-group. No males were represented among the IV- and VII-group individuals. The increasing dominance of the females with age suggests that the males are the less viable. The data on sexual maturity (p. 329) indicate, however, that the males mature earlier in life than do the females, and since the fishery concentrates on the spawning run (p. 307), the males are removed first from the lake, which results in a shift in the sex ratio of the older fish. The sex ratios may also fluctuate to some degree in the different areas of the lake or on different dates, since the percentage (50) of the I-group males was less at Lorain on August

14, 1929, than at Huron on July 1, 1929. When the data of all age groups are combined the sex ratio is approximately 50 : 50.

VIII. AGE AND SIZE AT SEXUAL MATURITY

Since the 1927 and 1929 data on sexual maturity were consistent and supplementary, they were combined for each age group and arranged in Table XIV according to total lengths. All the 1927 materials were collected at Sandusky, Ohio, and all the 1929 data at Huron, Ohio, on July 1, 1929. All the 0-group white bass, which were collected in 1927, were immature. Ninety-one per cent of the I-group fish were immature. All the mature individuals of this group were males captured in 1927. Virtually all the I-year immature fish, 7.5 inches and larger, were also taken in this year; nearly all the smaller specimens were collected in 1929. Fifty-eight per cent (6 males, 8 females captured in 1929) of the II-group and all older individuals were sexually mature. The majority of the fish (sexes combined) do not begin to develop sexually until their third summer or to spawn until the age of three years, when they average 10.9 inches in total length (Table VII). The males, however, begin to reach maturity in the second summer, a year earlier than do the females, and to spawn at two years, when they average approximately 8.2 inches in total length.

The data in the column at the extreme right of Table XIV indicate that all white bass under 7.5 inches, total length, were immature. Not until the fish reached the length interval 9.5 10.0 inches did the majority of a size class show developing sex organs. All specimens larger than 10 inches, total length, were recorded as maturing. Eighty per cent of the 452 white bass taken in trap nets were immature.

The data suggest that, in order to protect adequately the majority of the white bass that have not yet spawned, a legal size limit of 11 inches, total length, must be established. The present size limit is 9 inches in Ohio and Michigan. Of the 88 sampled fish of legal length 20 specimens, or 23 per cent, were immature. Sixty-nine per cent of the 88 legal fish were less than 11 inches in length. An unknown number of these, although maturing, had never spawned before. The available data indicate, then, that somewhere between 23 and 69 per cent of the fish taken legally in commercial impounding nets have never spawned.

TABLE XIV

NUMBER AND PERCENTAGE (IN PARENTHESES) OF IMMATURE AND MATURE LAKE ERIE WHITE BASS IN THE COMBINED COLLECTIONS TAKEN AT SANDUSKY, OHIO, IN 1927 AND AT HURON, OHIO, ON JULY 1, 1929, ARRANGED ACCORDING TO AGE AND TOTAL LENGTH

Total length interval in inches *	Standard length interval in mm.	Age group									
		0	I		II		III	IV	VII	0–VII	
		I †	I	M †	I	M	M	M	M	I	M
4.5–5.0	91–100	1	3	0	..	..	..	..	..	4	0
		(100.0)	(100.0)	(0.0)	..	..	..	..	..	(100.0)	(0.0)
5.0–5.5	101–110	..	4	0	..	..	..	..	..	4	0
		..	(100.0)	(0.0)	..	..	..	..	..	(100.0)	(0.0)
5.5–6.0	111–121	3	43	0	..	..	..	..	..	46	0
		(100.0)	(100.0)	(0.0)	..	..	..	..	..	(100.0)	(0.0)
6.0–6.5	122–131	..	85	0	..	..	..	..	..	85	0
		..	(100.0)	(0.0)	..	..	..	..	..	(100.0)	(0.0)
6.5–7.0	132–141	..	55	0	..	..	..	..	..	55	0
		..	(100.0)	(0.0)	..	..	..	..	..	(100.0)	(0.0)
7.0–7.5	142–151	..	19	0	..	..	..	..	..	21 ‡	0
		..	(100.0)	(0.0)	..	..	..	..	..	(100.0)	(0.0)
7.5–8.0	152–161	..	34	2	1	0	..	..	..	35	2
		..	(94.4)	(5.6)	(100.0)	(0.0)	..	..	..	(94.6)	(5.4)
8.0–8.5	162–171	..	47	1	3	0	..	..	..	52 ‡	1
		..	(97.9)	(2.1)	(100.0)	(0.0)	..	..	..	(98.1)	(1.9)
8.5–9.0	172–181	..	35	20	2	1	..	..	..	38 §	21
		..	(63.6)	(36.4)	(66.7)	(33.3)	..	..	..	(64.4)	(35.6)
9.0–9.5	182–192	..	13	6	2	5	..	..	..	15	12 §
		..	(68.4)	(31.6)	(28.6)	(71.4)	..	..	..	(55.6)	(44.4)

9.5–10.0	193–202	..	3	3	2	4	..	..	..	5	7
		..	(50.0)	(50.0)	(33.3)	(66.7)	..	..	..	(41.7)	(58.3)
10.0–10.5	203–212	..	..	..	0	3	6	..	..	0	9
		..	..	..	(0.0)	(100.0)	(100.0)	..	..	(0.0)	(100.0)
10.5–11.0	213–222	..	..	..	0	1	11	1	..	0	13
		..	..	..	(0.0)	(100.0)	(100.0)	(100.0)	..	(0.0)	(100.0)
11.0–11.5	223–232	..	..	.	..	..	10	..	..	0	10
		..	..	..	..	..	(100.0)	..	..	(0.0)	(100.0)
11.5–12.0	233–242	..	..	..	..	..	10	..	..	0	10
		..	..	..	..	..	(100.0)	..	..	(0.0)	(100.0)
12.0–12.5	243–252	..	..	..	..	..	3	..	..	0	3
		..	..	..	..	..	(100.0)	..	..	(0.0)	(100.0)
12.5–13.0	253–262	..	..	..	..	..	1	1	..	0	2
		..	..	..	..	..	(100.0)	(100.0)	..	(0.0)	(100.0)
13.0–13.5	263–273	..	..	..	..	..	..	..	..	..	..
13.5–14.0	274–283	..	..	..	..	..	..	..	..	..	..
14.0–14.5	284–293	..	..	..	..	..	..	..	1	0	1
		..	..	..	..	..	..	..	(100.0)	(0.0)	(100.0)
14.5–15.0	294–303	..	..	..	..	..	..	..	1	0	1
		..	..	..	..	..	..	..	(100.0)	(0.0)	(100.0)
Total.....		4	341	32	10	14	41	2	2	360	92
		(100.0)	(91.4)	(8.6)	(41.7)	(58.3)	(100.0)	(100.0)	(100.0)	(79.6)	(20.4)

* The fish included within each total-length interval had lengths equal to the lowest and up to, but not including, the greatest length of the interval.

† I = Immature; M = Mature.

‡ Includes two fish for which no age was determined.

§ Includes one fish for which no age was determined.

IX. SUMMARY

1. The study on the age and growth of the Lake Erie white bass was founded on 1,869 fish taken in 1927, 1928, and 1929 in commercial trap nets and pound nets. The data on length-weight relationship were obtained from 4,904 specimens.

2. The direct-proportion calculated lengths were corrected for the differential growth in length of the body and the anterior radius of the scale by the formula given on page 309. Figure 1 provides a graphic view of the body–scale relationship.

3. Although all age groups from 0 to VII were represented in the samples, only 4.7 per cent of the fish were older than three years. Age groups I and II dominated in the catch. The 1926 year class dominated the collections made in 1927 and 1928, and the 1928 year class dominated in 1929.

4. Length frequencies of all fish combined exhibited a mode at 175 millimeters (8.6 inches, total length), which corresponded with that of the I-group fish. Eighty-seven per cent of the white bass varied between the 7- and 11-inch length intervals, and approximately 62 per cent of the individuals were below Ohio's legal size limit of 9 inches.

5. The females were only slightly larger than the males at corresponding ages. The differences did not appear to be significant.

6. The season's growth was virtually completed by the middle of October.

7. No differential growth existed among the white bass from different localities as the result of inhabiting various sections of the lake. With respect to growth the Lake Erie population may be considered homogeneous.

8. Differential growth occurred among the year classes. Both the first- and second-year growth improved progressively in the calendar years 1926 28. It is suggested that this change may possibly be associated with the great abundance of the 1926 year class — improved growth being inversely correlated with density of population.

9. The greatest growth in length occurred in the first year, followed by a progressive decline through the seventh year.

10. The greatest increment in weight occurred in the third year, the smallest, in the first. If we are to take advantage of the rapid

growth in weight, the white bass should be protected by an 11-inch legal size limit. The present size limit in Ohio and Michigan is 9 inches.

11. An apparent compensation in growth occurred in the third year of life.

12. An equation has been developed that expresses with considerable accuracy the length-weight relationship. The curve expressing this relationship has been so drawn on the graph that lengths may be converted readily from standard to total and vice versa, and weights from grams to ounces and vice versa. The length-conversion factors exhibited no significant or consistent variation with a change in the length of the fish. A single factor was therefore employed for each type of conversion.

13. The coefficient of condition, K, did not vary significantly with the sexes, age groups, localities, calendar years, or months of the growing season. The K value rose in November, and also showed some correlation with the length of the fish. The K remained fairly constant up to a length of 192 millimeters, then increased gradually up to a length of 278 millimeters, when it dropped. The high average value of K (2.37) indicates that the white bass is robust in form.

14. The sex ratio of all fish combined was approximately 50 : 50, although the percentage of females increased with age, owing primarily to the capture of the younger and earlier-maturing males.

15. The majority of the white bass (sexes combined) began to spawn at the age of three years, when they averaged nearly 11 inches in total length. Males began to spawn a year earlier than the females, that is, at the age of two years and an average length of 8.2 inches. To provide adequate protection for the nonspawned fish, a legal size limit of 11 inches, total length, must be established. (See also item 10.) Between 23 and 69 per cent of the white bass taken legally in commercial impounding nets have in all probability never spawned.

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